Unilateral Neglect as "Temporal Diplopia"

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To Charles

Declaration of Authorship

I, **Karen Budewig**, declare that the thesis of the title "Unilateral Neglect as 'Temporal Diplopia' " is my own work.

Signature

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ABSTRACT OF THESIS

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This thesis presents a new model of unilateral neglect. The theory is based on existing and novel empirical data collected in the current study which involved stroke patients with and without neglect.

"Patients with unilateral spatial neglect ... fail to report, respond or orient to stimuli presented on the side of space contralateral to the lesion" (Làdavas, 1994, p.155). However, numerous studies have established that neglect is far more complex than the above definition suggests. Many subtypes and dissociations of neglect have been described. It is now increasingly recognised that the wide range of phenomena classified as symptoms of neglect can not be fully covered by a single explanatory model.

Halligan and Marshall (1992) have called for the exploration of "principles" of malfunction in neglect patients. In this thesis, we have provided such a principle. The core of the thesis is a new model of unilateral neglect, the "temporal diplopia" theory. It is strictly constrained by neuroanatomical and electrophysiological evidence. Our model claims that the underlying pathology in unilateral neglect is abnormal temporal integration and binding of information due to desynchronised neuronal activity. Disruptions in the temporal domain lead to impaired processing within the damaged hemisphere and between the two hemispheres.

The empirical data presented in this thesis were compatible with the predictions of the "temporal diplopia" theory and the hypothesis that processing in the damaged hemisphere might be slowed down. The claims made by the theory were explored in a time perception, rhythm perception and inspection time paradigm. We have illustrated the explanatory power of our theory by unifying existing empirical evidence of neglect. Stimulus properties in neglect dyslexia were explored. Furthermore, we addressed the general 'binding' problem of body schemata and the disintegration of body schemata due to disrupted temporal neuronal processing.

Our thesis is the first to investigate extensively the temporal aspects of information processing in unilateral neglect patients. Abnormal temporal processing appears to be a fundamental problem and it has been associated with a number of neuropsychological and psychiatric disorders such as dyslexia, dysphasia, autism and schizophrenia. Why temporal malfunction leads to different clinical pictures in different patient groups is a question that warrants future exploration.

Contents

Chapter One

Introduction and some meta-theoretical considerations on unilateral neglect

Although the first case reports of unilateral neglect and neglect dyslexia were published in the second half of the last century (Jackson, 1876; Anton, 1883; Pick, 1898; quoted by Halligan & Marshall, 1993c), it has only been since the 1970s that the research community has rediscovered neglect (Halligan & Marshall, 1993c).

"Patients with unilateral spatial neglect ... fail to report, respond or orient to stimuli presented on the side of space contralateral to the lesion" (Làdavas, 1994, p.155). However, numerous studies have established that neglect is far more complex than the above definition suggests. Many subtypes and dissociations of neglect have been described (for a review see Halligan & Marshall, 1993c). It is now increasingly recognised that the wide range of phenomena classified as symptoms of neglect can not be covered by a single diagnostic or explanatory model (e.g. Barbieri & De Renzi, 1989; Halligan & Marshall, 1992, 1993c, 1994b; Brewer, 1994; Heilman et al., 1994; Kinsbourne, 1994; Mattingley & Bradshaw, 1994; Mesulam, 1994; Milner & Harvey, 1994; but see Berti & Rizzolatti, 1994).
Robertson (1994, p.199) has summarised the state of affairs as follows: "Neglect behaviour can reflect deficits in a variety of mechanisms that together operate to produce awareness, attention, perceptual organisation, spatial representation, and preparation for action in space, in sum, much of cognition. So, in order to explain neglect, we need a theory of cognition and consciousness".

All existing theories seeking to unravel the mystery of neglect have addressed these aspects of cognition in one way or the other (for a review see next chapter). In the last years attentional and representational accounts of neglect have dominated the

discussion and vast quantities of empirical data have been amassed. However, the theoretical debate remains unresolved. Recently a certain sense of frustration has led to calls to progress from undoubtedly useful empirical accounts to dynamic computational models that are powerful enough to make quantitative predictions (Humphreys & Riddoch, 1994; Young, 1994). There are not many models that satisfy these desired criteria: Chatterjee (1995) developed a power function to describe the relationship between line length and displacement in line-bisection tasks (see also Halligan & Marshall, 1989). Smith (1994) proposed a mathematical approach to compare performance parameters between the line bisection and the star cancellation tasks, clinical tests that unilateral neglect patients are commonly asked to perform. As for connectionist models, Monaghan and Shillcock (1998) have successfully modelled the cross-over effect in unilateral neglect. Mozer and Behrman (1990) put forward a computational framework to account for neglect dyslexia and, in a series of publications, Pouget and Sejnowski (1995, 1996, 1999) developed a model of neglect that was rooted in the response properties of the parietal neurons.

In this thesis, we present a theory of neglect that does not qualify as a model capable of powerful quantitative descriptions. Our work makes a further contribution to the dramatic expansion in the number of empirical studies. It is therefore not the kind of work Humphreys and Riddoch (1994) and Young (1994) had in mind. However, our model is tightly constrained by neuroanatomical and neurophysiological evidence. In our mind, before any practical work on a neuropsychological disorder can begin, the associated neuro*physiological* changes should be clearly described. This approach has led to the development of a theory that has attempted to translate existing low-level neuropathology into a coherent framework of perceptual and cognitive impairment. However, at no point we will claim to have produced a unifying account of neglect.

The following chapter of the thesis presents a comprehensive review of unilateral neglect and neglect theories. Chapter three explores in detail issues of selective attention as the most popular theories of neglect stress attentional factors in neglect.

We put special emphasis on neuroanatomical and -physiological correlates of visuo-spatial attention.

Chapter four presents our theory of neglect which forms the core of the thesis. The chapter starts with a detailed analysis of neuropathological changes after stroke. We claim that hemispheric processing is slowed down after a cerebro-vascular accident. Analogies are drawn between strabismus, binocular rivalry and saccadic suppression to illustrate a general processing mechanism: Incompatible information is suppressed by the brain. We demonstrate that many aspects of neglect can be addressed by postulating impaired interhemispheric processing due to interhemispheric desynchronisation. Information processed in the ipsilesional hemisphere is temporally incompatible with information processing in the intact hemisphere. Consequently, information in the damaged side is excluded from conscious processing, i.e. is suppressed. Similarly, neural centres in the damaged hemispheres are out of synch with each other. The binding and integration of information in the ipsilesional hemisphere are disrupted. The explanatory power of the model is discussed in detail at the end of the chapter.

Chapters five to nine present the empirical data of the thesis: Chapter five explores time perception in stroke patients with and without neglect. For the first time a study is presented that has examined neglect patients within the framework of scalar time theory (Gibbon (1977; Gibbon, 1981a,b; Gibbon & Church, 1984; Gibbon et al., 1984) and the bisection time paradigm (Nichelli et al., 1995, 1996). Chapter six investigates rhythm perception in neglect and non-neglect patients by introducing a novel methodology. Chapter seven describes the analysis of the data obtained in a modified inspection time experiment (Hellige et al., 1989). The rationale of the experiments described in chapters five, six and seven is to explore the claim made in chapter four that the ipsilesional hemisphere is slowed down in its processing speed.

Chapter eight starts with a review of neglect dyslexia and discusses the observed symmetry effects of lexical material in neglect patients (Shillcock et al., 1998) in connection with completion phenomena. The objective of this chapter is to analyse interhemispheric interaction in connection with specific predictions made by our theory.

Chapter nine describes a single case study of a neglect patient who has reported the experience a supernumerary limb. We present a review of similar cases in the neglect literature and discuss supernumerary limbs in the framework of existing phantom limb theories. The investigation is concerned with the general 'binding' problem of body schemata. Furthermore, we address the relationship between perception and the body image.

The last chapter provides a final discussion and ends with the conclusion that many aspects of neglect can be accounted for in a principled way by postulating impaired interhemispheric and intrahemispheric desynchronisation due to slowing down of neuronal processing speed.

Chapter Two

Unilateral neglect and extinction
A Review

This chapter will provide a review of the existing neglect literature. We will discuss the neuroanatomical correlates of unilateral neglect based on evidence from anatomo-clinical correlation studies, followed by the presentation of definitions and the taxonomy of neglect and its related disorders.

An introduction to the general clinical manifestations of unilateral neglect and associated deficits will prepare for the discussion of the existing theories which will be illustrated with further clinical details of unilateral neglect. In the final section, we will present data on the recovery of neglect and will conclude the chapter with a review of the extinction phenomenon.

1. Introduction

"Neglect is the failure to report, respond or orient to novel or meaningful stimuli presented to the side opposite a brain lesion when this failure cannot be attributed to either sensory or motor defects" (Heilman et al., 1993, p.279).

That the phenomenon of neglect extends beyond this seemingly clear-cut definition is reflected by the terminological confusion in the relevant literature. Halligan and Marshall (1993c) who presented a historical review on neglect collected the following terms that have been used in the past to characterise neglect: "neglect of the left half of visual space (Brain, 1941); unilateral visual inattention (Allen, 1948); unilateral spatial agnosia (Duke-Elder, 1949); imperception for one half of external space (Critchley, 1953); amorphosynthesis (Denny-Brown & Banker, 1954); left-sided fixed hemianopia (Luria, 1972); hemi-inattention (Weinstein & Friedland, 1977); hemi-neglect (Kinsbourne, 1977b); unilateral neglect (Hécaen & Albert, 1978); hemi-spatial agnosia (Willanger, et al., 1981); contralesional neglect (Ogden,

1985b); dyschiria (Bisiach & Berti, 1987) and directional hypokinesia (Coslett et al., 1990)" (Halligan and Marshall,1993c, p.5).

Heilman et al. (1993) proposed to divide neglect into the following related disorders: (1) sensory neglect, (2) spatial neglect (3) personal neglect, (4) motor neglect, (5) allesthesia and allokinesia, (6) anosognosia and (7) extinction.

For future reference, unless explicitly specified, the term unilateral neglect will be used in this thesis to refer to neglect as a unitary syndrome basically for pragmatic reasons because the majority of studies have not tried to differentiate the various components of neglect. We are well aware of the problem that this approach carries (Barbieri & De Renzi, 1989; Cubelli et al., 1991; Halligan & Marshall, 1992), as will be discussed at a later point.

2. The anatomical substrate of unilateral neglect in humans

In this section, studies will be reviewed that have examined the correlation between the neuroanatomy of cerebral damage and the clinical picture of unilateral neglect. The findings in these studies have been based upon post-mortem examinations and modern radiological techniques such as CT- or MRI-scans. The animal literature will not be considered in this thesis. The reader is referred to Gaffan and Hornak (1997) for a recent review.

An analysis of the functional neuroanatomy and general neurophysiological cerebral changes in stroke patients will be provided in chapter five.

2.1. Left versus right hemisphere: The incidence and severity of unilateral neglect

One of the least debated aspects of unilateral neglect is the claim that neglect symptoms are more frequent and severe after right hemisphere damage (Brain, 1941; Critchley, 1950; McFie & Zangwill, 1960; Arrigoni & De Renzi, 1964; Benton, 1969; Faglioni et al., 1971; Gainotti & Tiacci, 1971; Gainotti et al., 1972; Chedru, 1976; Schenkenberg et al., 1980; Mesulam, 1981; Denes et al., 1982; Kinsbourne, 1987; Massironi et al., 1988; Heilman et al., 1993; Spiers et al., 1993).

Hécaen (1972, quoted by Vallar, 1993) examined a large population of unilaterally brain damaged patients. Contralesional neglect was diagnosed in 56 out of 179 patients with right hemisphere lesions (32%) whereas only one patient out of the 286

left brain damaged patients showed signs of neglect (< 1%). Bisiach et al. (1984) found contralesional neglect in 15 out 56 right hemisphere patients (28%). Neglect was not diagnosed in a single patient out of the 51 left brain damaged patients. Similar figures were reported in a study by Massironi et al. (1988) where 40% of right hemisphere patients showed neglect which was absent in the left hemisphere group.

However, there are some studies that do not fit completely into this generally accepted picture. Albert (1973) tested 30 left and 36 right neglect patients in a cancellation task. The results showed that the side of hemispheric lesion had no influence on the incidence of neglect. Thirty seven percent of the patients were classified as suffering from left neglect and 30% of the subjects from right neglect. However, neglect was more severe after right hemisphere damage. Similarly, Ogden (1985) tested nine left and nine right hemisphere patients in a mental imagery task. In the left brain damaged group, seven patients suffered from neglect whereas only three patients with right hemisphere damage displayed neglect symptoms. The severity of neglect, though, proved to be more marked in the right neglect group compared to the left neglect subjects in one of the two conditions. This result received more weight in a different study by Ogden (1985b) where much greater numbers of patients were involved. One hundred and one patients with unilateral lesions were tested in a neglect battery. Exactly 50% of left brain damaged patients showed neglect compared to only 45 % in the right hemisphere group. There were no significant differences in severity scores between the two groups on four out of five tasks. However, the right hemisphere subjects showed neglect on more tests than the left brain damaged group.

To summarise, in general, agreement exists as far as the severity of neglect symptoms after right hemisphere damage is concerned but there is no unified position with regard to incidence. Zarit and Kahn (1974) identified twice as many neglect patients in the right hemisphere group but interpreted these differences as artifacts due to the recruitment methods and due to the fact that neglect is more severe in left neglect. Most of the untestable patients in the study had suffered damage to the left hemisphere and were aphasic (see also Ogden, 1987) .

Another problem in patient recruitment practice is the tests that are used to establish neglect. The clinical tests are not standardised and some leave much to be desired with regards to sensitivity (Massironi et al., 1988; Halligan et al., 1989) with the star cancellation task being the most sensitive measure of neglect (Halligan et al., 1989; Stone et al., 1992). A further point that deserves mention in this context is the homogeneity of the patient group as far as the etiology of the lesions is concerned. Brain damage due to a tumor is associated with different neurophysiological changes than a space occupying lesion caused by a burst aneurysm. Furthermore, since the most florid symptoms of neglect tend to disappear within weeks and if, as the data suggest, the severity of neglect is more pronounced after right hemisphere damage, the number of patients with right neglect should drop more quickly the longer the interval between onset of illness and time of testing (Denes et al., 1982).

To conclude, the severity of neglect appears to be more marked after right hemisphere damage. However, exact figures on the incidence of right versus left neglect will remain questionable until major shortcomings in recruitment and methodology that make a direct comparison between the left and the right hemisphere patient groups very difficult are overcome. Ogden (1987, p.229) has even claimed that "the majority of patients with acute unilateral lesions have some degree of visuospatial neglect", irrespective of the hemispheric side of damage, as long as the tests are sensitive enough. Nevertheless, if, after remedying the critical methodological points, a higher incidence of left neglect emerged, the result would not surprise given the 'visuo-spatial' superiority of the right hemisphere (Bradshaw & Nettleton, 1981).

2.2. Cerebral lesion sites in unilateral neglect

2.2.1. Cortico-subcortical lesions

Before the age of modern non-invasive radiological techniques, unilateral neglect had been strongly associated with parietal lobe damage (Brain, 1941; Critchley, 1950; McFie et al., 1950). More recently, many studies have provided evidence for extra-parietal lesion sites in the neglect syndrome including non-hemispheric sites like the corpus callosum (Kashiwagi et al., 1990). For instance, both the right frontal lobe (Heilman & Valenstein, 1972; Stein & Volpe, 1983; Ogden, 1985b; Vallar &

Perani, 1986; Bisiach et al., 1990; Daffner et al., 1990; Tégner & Levander, 1991; Bottini et al., 1992; Samuelsson et al., 1997) and the left frontal lobe (Damasio et al., 1980) have been reported to be involved in neglect. In this context, Ogden (1985b) reported an interesting association between frontal lesions and right neglect, a finding which has not been replicated, though. From anatomo-clinical correlation studies there is some evidence that the more common cortical lesion site clusters around the retro-rolandic area involving the temporo-parieto-occipital junction (Battersby et al., 1956; Ruff et al., 1981; Vallar & Perani, 1986, 1987; 1988; Samuelsson, 1997). Within the retro-rolandic area, the infer-posterior area of the right parietal lobe appears to be of particular significance (Bisiach et al., 1981; Vallar & Perani, 1986; Mattingley et al., 1998, but see Watson et al., 1981). On the other hand, Egelko et al. (1988) reported a lack of specificity in the relationship of the site of cerebral damage and left unilateral neglect. Also, a recent study that examined right hemisphere stroke patients concluded that left neglect at the acute stage was strongly associated with lesions involving the middle temporal gyrus and/or the temporo-parietal white matter (Samuelsson et al., 1997). The role of subcortical lesions will be discussed in the next section.

2.2.2. Subcortical lesions

Unlike Samuelsson et al.'s (1997) findings, Vallar and Perani (1986) claimed that lesions confined to the subcortical white matter rarely produce neglect. According to the results, neglect was much more frequently associated with lesions to the gray nuclei like the thalamus and the basal ganglia. In a later study, Perani et al. (1987) presented incidence figures for neglect of 66% after thalamic lesions, 40% after basal ganglia lesions and 40% after white matter damage.

In humans, it is difficult to establish which of the subcortical structures are connected most tightly with neglect since the lesions are very rarely confined to one structure. Some single case studies have presented neglect patients whose lesion was restricted to one particular area, like the posterior limb of the right internal capsule (Ferro & Kertesz, 1984) or the thalamus (Watson & Heilman, 1979). In most cases, however, the lesions involve several structures. In a study by Ferro et al. (1987), the most severe neglect cases were caused by a large caudate-putameno-capsular infarction.

Several other studies have presented cases of contralesional neglect after lesions involving both the white matter and the gray nuclei (Damasio et al., 1980; Watson et al., 1981; Healton et al., 1982; Stein & Volpe, 1983; Fromm et al., 1985; Perani et al., 1987; Bogousslavsky et al., 1988).

In summary, anatomico-clincal correlation studies on unilateral neglect have pointed towards a particular role of the inferior-posterior area of the parietal lobe and the gray nuclei involving the thalamus and the basal ganglia. However, the great variety of lesions sites that have been reported to cause unilateral neglect suggests "the neural correlates of spatial representation and awareness should be conceived of in terms of complex cortico-subcortical neural circuits" (Vallar, 1993, p.52; see also Damasio et al., 1980, Mesulam, 1981). The anatomical data also lend support to the preliminary suggestion that unilateral neglect might not be a unitary syndrome. This issue will be taken up again in the next section when the clinical picture of neglect and its related disorders will be analysed.

3. The clinical picture of unilateral neglect

Symptoms of florid neglect can be discovered by simply observing the patient's spontaneous behaviour or during routine clinical examination. The patient may sit slumped in the chair with the head and eyes deviated to the contralesional hemispace. In cases of severe extrapersonal neglect, the patient may fail to respond altogether when addressed from the contralesional hemispace or may search for the speaker on the ipsilesional side. Potatoes might not be eaten from the contralesional side of the plate and, if the patient is mobile, he/she might get lost during explorations of the ward since landmarks from the contralesional side of space are not used.

In the following sections, the clinical picture of neglect will be presented. Heilman et al. (1993) divided neglect into (1) sensory neglect, (2) personal neglect, (3) spatial neglect, (4) motor neglect, (5) allesthesia and allokinesia, (6) anosognosia and (7) extinction to simultaneous stimuli. This taxonomy of neglect and its components will serve as a structural guide but will be altered and extended where necessary.

3.1. Components of neglect and related disorders: Definitions and dissociations

3.1.1. Sensory neglect

"Sensory neglect or inattention refers to a deficit in awareness of contralateral stimuli in patients ... with lesions in locations other than primary sensory areas or sensory projection systems" (Heilman et al., 1993, p.279).

Any sensory modality can be affected. The patient might show neglect in several modalities at the same time or neglect may be present in one modality only (Beschin et al., 1996). Even within one modality, dissociations of neglect have been described depending on the nature of the information processing (Guariglia et al., 1993). The issue of dissociations is important with regards to the question of whether neglect is due to a supra-modal or a modality specific deficit. Suffice it to say at this point that none of the theories of neglect can accommodate a modality-specific view apart from theories that have defined neglect as a sensory impairment and Rizzolati and Camarda (1987) who proposed a model of spatial attention consisting of a series of circuits largely independent from each other. Theories of neglect will be dealt with in detail at a later point.

Young et al. (1990) presented a single case study of a left neglect patient who displayed neglect towards left-sided features of facial expression and of resemblance between faces. On the other hand, the patient was able to allocate left or right half-stimuli correctly into categories "human face", "dog face" or "tree". Guariglia et al. (1993) documented a dissociation of neglect symptoms between visual imagery and objects that were presented in the near and far space. The patient had suffered a right hemisphere injury and showed neglect only to the left side of mental images whereas his scores in visuo-spatial test were within normal limits. Vallar et al. (1991) investigated a left neglect patient who did not respond to tactile stimulation of his contralesional body part but did not show neglect for the left half of his body which suggests intact proprioceptive perception. Other studies have described dissociations between modalities, for instance, between the olfactory and tactile modalities (Bellas et al., 1988) and between the auditory and visual modalities (De Renzi et al., 1989b).

3.1.2. Personal neglect *and other reference frames in neglect*

According to Heilman et al. (1993), if a patient suffers from personal neglect, he/she may feel that a contralesional extremity does not belong to him/her or, in the case of milder neglect, the patient might not dress or groom the contralesional side.

Other studies have shown that neglect extends beyond the personal space and can produce dissociations with regard to personal/peri-personal and extra-personal[1] space. Bisiach et al. (1986) reported a double dissociation in left neglect patients between tasks assessing the personal and 'extra-personal' space. In the former test, patients were required to reach with the ipsilesional hand to different body parts on the contralesional side. The task assessing 'extra-personal space' was a simple cancellation task at a normal reading distance. Beschin et al. (1996) identified two right hemisphere patients as showing neglect for far peri-personal but not in near peri-personal space in a tactile maze test. Halligan and Marshall (1991c) presented a single case study of a left neglect patient who showed severe neglect when a line bisection task was performed at a viewing distance of 450 mm which was within the peri-personal space. When the patient was positioned at a distance of 2.44 m from the board which was outside the peri-personal space, his bisection score was normal or improved compared to the peri-personal condition. A similar but reversed effect was demonstrated by Shelton et al. (1990; see also Cowey et al., 1999). Shelton et al. (1990) reported the case of a patient with bilateral inferior temporal lobe damage who extinguished distant stimuli in the upper vertical space on simultaneous presentation of a stimulus in the distant lower field. However, when the upper stimulus was brought nearer the patient, it was no longer extinguished on double stimulation. The results in Shelton et al.'s study (1990) addressed a different question of neglect. Does neglect emerge in spatial dimensions other than in the classical horizontal dimension? Shelton et al.'s patient (1990) also showed neglect of the upper vertical space in a line bisection task where he misbisected vertical lines below

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[1] The terms 'peri-' and 'extra-personal' space are not used in a consistent way in the literature. For Bisiach et al. (1986) 'extra-personal' equals non-personal, i.e. the concept includes peri-personal space. On the other hand, Halligan and Marshall (1991c) defined peri-personal space as 'near' and extra-personal as 'far' space whereby in the near-space condition, the patient had to bisect lines at a distance of 45 cm and in the far-space condition at a distance of 2.44 m. Mennemeier et al. (1992) conducted a line bisection task in three peri-personal space conditions: in near (the paper with the lines adjacent to the patient's body), middle (30 cm from the patient's body) and far peripersonal space (60 cm from the patient's body).

the actual midpoint. Mennemeier et al. (1992) described a single case of a patient who had suffered bilateral parietal lobe lesions. In a line bisection task, the patient showed left horizontal, near radial and inferior vertical neglect. It was the same patient who had been examined four years earlier by Rapcsak et al. (1988). Inferior vertical neglect in a line bisection task had been established at the time. Both Rapcsak et al. (1988) and Mennemeier et al. (1992) concluded that bilateral lesions were associated with neglect in the radial and vertical dimension.
However, Halligan and Marshall (1991b) demonstrated left and inferior vertical neglect in a patient with right hemisphere brain damage bisecting horizontal and vertical lines and left and superior vertical neglect involving patients from a different study (Halligan & Marshall, 1993; see also Halligan & Marshall, 1994). Similar results were presented in a study by Gold et al. (1994) where a patient with right-sided hemispheric lesions displayed left and inferior vertical neglect in a cancellation task.

To summarise, neglect may manifest itself along all three dimensions within the personal, peri-personal and extra-personal space and shows various dissociation patterns. The next question to be raised at this point concerns which frames of reference or spatial co-ordinate systems that code spatial location exist and can be affected by unilateral neglect. Research on neglect has investigated this question with regard to a distinction between allocentric and egocentric space. Allocentric co-ordinates specify locations of an object independent of the viewer, whereas the egocentric frame of reference represents stimuli relative to the viewer. The egocentric system has to be further divided into a retinotopic, head-centred and body-centred co-ordinate system whereas the allocentric system incorporates an environment-centred frame of reference and object-centred co-ordinate system. In the environment-centred system, objects are coded relative to the environment and, if the viewer changes position, the representation of the objects is not altered. In the object-centred system, the location and parts of an object is represented relative to the whole object. Again, position changes of the viewer do not change the object-centred representation but the representation is also stable, unlike in the environment-centred reference frame, when the object is turned upside down for

example. In an object-centred co-ordinate system, a receiver is always at the top of a telephone (Farah et al., 1990).

Various neglect studies have tried to disentangle these different co-ordinate systems. Heilman and Valenstein (1979) demonstrated that neglect was tied to the body midline. When lines were bisected in the left hemispace, left neglect patients had a higher deviation score compared to lines they bisected in the right hemispace. The same result was reported by Karnath et al. (1991) who examined a group of left neglect patients in a reaction time task. The spatial relation between orientation of head and trunk midlines and location of the target stimuli was systematically varied while holding the retinal projection of the stimuli constant. Turning the body to the left so that the stimuli were projected into the ipsilesional hemispace improved reaction times to left relative stimuli. Kooistra and Heilman (1989) demonstrated neglect which was tied to the body midline but only in the condition when the left neglect patient directed the eyes to the left side while maintaining head position aligned with the body. In this condition, the two visual hemifields were tested in the right hemispace with respect to the body midline. Although the retinotopic co-ordinates remained the same, left visual field stimulus detection improved significantly. However, in a line bisection task the neglect patient failed to improve the performance when the line was placed in the right hemispace with free head and eye movement.

In a tactile exploration task, Bisiach et al. (1985) demonstrated that left neglect was anchored both to the midsagittal body plane and the line of sight (i.e. either retinotopic or head-centred co-ordinates because head and eye positions were not dissociated from each other). Farah et al. (1990) examined a group of left neglect patients to explore which representational frame was impaired. The retinotopic, environmental and object-centred reference frames were disentangled from each other by rotating either the viewer or the stimulus object systematically. The results suggested that the patients' neglect was defined with respect to both retinotopic and environment-centred frames of reference but not with respect to object-centred co-ordinates. A similar result was presented by Làdavas (1987) and Gazzaniga and Làdavas (1987) who concluded that the left neglect in the patient group was related

both to retinotopic and environment-centred frames of reference (see also Calvanio et al., 1987). The data are consistent with the work of Pouget and Sejnowski (1995) who have questioned that the parietal cortex translates the spatial co-ordinates of an object into a particular frame of reference but "instead computes a general purpose representation of the retinal location and eye position from which any transformation can be synthesized by direct projection" (Pouget & Sejnowski, 1995, p.1). It is therefore predicted that unilateral neglect symptoms should emerge in multiple reference frames in single patients (see also Tipper & Behrmann, 1996).

The hypothesis that neglect might also operate on object-centred co-ordinates was originally based on the peculiar drawing patterns observed in some neglect patients. Typically, neglect patients omit the contralesional details when copying a scene. Sometimes, however, they might omit the contralesional side of each object of the scene irrespective of their location in the patients' drawing (e.g. Apfeldorf, 1962; Gainotti et al., 1972; Halligan & Marshall, 1993d). In a same/different task Driver and Halligan (1991) asked a patient with severe left-sided neglect to judge two elongated nonsense shapes, presented one above the other. When the two shapes were aligned with the patient's midsagittal body plane, the left side of the shapes was neglected. When the shapes were both rotated clockwise and anti-clockwise by 45 degrees, the patient continued to miss the differences on the left side although these differences were presented on the right of the midsagittal plane. This result was interpreted as evidence that neglect can be associated with object-centred co-ordinates which operated relative to the principal axes of the shapes. Driver et al. (1994) later criticised this interpretation as too rash since the same results might emerge due to neglect anchored to an egocentric reference frame. "One simply needs to assume that egocentric neglect arises in relative terms ... rather than applying globally to an entire hemifield defined by an egocentric midline" (Driver et al., 1994, p.1356). To control for interference from an egocentric reference frame, shapes with ambiguous axes were chosen as stimuli that allowed manipulating the location of target information in axis-based co-ordinates while target information was kept constant in egocentric co-ordinates. Three left neglect patients were tested. The results provided further support for Driver and Halligan's (1991) preliminary interpretation of object-centred neglect relative to the object's principal axis.

To conclude, neglect can be tied to different reference frames. It is not clear, though, to what extent each co-ordinate system contributes to neglect, whether different types of neglect are involved, associated with different cerebral lesion sites, and to what extent various task requirements influence the results.

3.1.3. Spatial neglect and motor neglect

According to Heilman et al. (1993), spatial neglect is the failure of patients to "act in contralesional body centred space, or ... to act on the left side of stimuli" (Heilman et al., 1993; p.285). Because emphasis is put on the motor component, spatial neglect is subsumed here under the heading of an impairment on a motor level.

Now the terminology becomes confusing again. Heilman et al. (1993) defined motor neglect as either hemispatial or directional. Others make a clear distinction between motor neglect as underutilisation of the contralateral limb (Laplane & Degos, 1983; Bisiach et al., 1990) and directional hypokinesia/akinesia as reluctance or failure "to initiate or carry out motor activities toward the contralesional side of egocentric space, irrespective of the side of the limbs involved in such activities" (Bisiach et al., 1990, p.1278). Accordingly, spatial neglect is an aspect of motor neglect following Heilman et al.'s (1993) definition or describes directional hypokinesia/akiniesia in Bisiach et al.'s (1990) sense.

However, a deficit on a motor level seems to be an established factor of neglect and there are multiple studies that have described dissociations of motor and sensory components of neglect (Laplane & Degos, 1983; Bisiach et al., 1990; Daffner, 1990; Mijovic, 1991; Tégner & Levander, 1991; Liu et al., 1992; Bottini et al., 1992; Beschin et al., 1996).

3.1.4. Allesthesia and allokinesia

Heilman et al. (1993) quoted Obersteiner (1882) as the researcher who first coined the word allesthesia. According to Meador et al. (1991), however, who reviewed the history of the concepts of allochiria and allesthesia, Obersteiner (1882) was the first to introduce the term allochiria not allesthesia. Allochiria describes the mislocation of sensory stimuli to the corresponding opposite half of the body or space. Stewart

(1894) later documented a similar phenomenon where stimuli are displaced to a different part of the same limb and called it allachaesthesia (i.e. allesthesia).
Obersteiner (1882) presented the first case of allochiria in the tactile modality of three patients who suffered from myelopathy and one patient from a disorder of hysterical nature. Later allochiria was associated with a variety of pathologies but most frequently with tabes dorsalis or hysteria (Meador et al., 1991). A possible case of tactile allochiria in a neglect patient (Zutt, 1931) was quoted by Critchley (1949). Transpositions of stimuli from the contralesional to the ipsilesional space have also been reported in the auditory modality (Di Pellegerino & De Renzi, 1995), in visual mental representations (Guariglia et al., 1993) and in drawing tasks (Halligan et al., 1992; patient K.R. in this study).
Allokinesia describes a related phenomenon in movement when for example a patient moves the ipsilesional limb although he/she was asked to move the contralesional extremity (Heilman et al., 1993).

3.1.5. Anosognosia

Anosognosia characterises the unawareness of any illness and disability and may exist without generalised intellectual impairment (Förstl et al., 1993). The term was first coined by Babinsky (1914; quoted by Bisiach et al., 1986b).
Cutting (1978) studied a group of 100 unilateral acute stroke patients and found anosognosia, i.e. the denial of the patient's hemiplegia, in 58% of left hemiplegics and 14% of right hemiplegic patients. Other anosognostic phenomena were reported and included a variety of abnormal beliefs about the affected side of the body like feelings of non-belonging, supernumerary limbs and hatred or lack of appropriate concern for the paralysed side. These symptoms related to anosognosia will be dealt with in detail in chapter seven that presents a patient with a supernumerary limb. The incidence figures regarding laterality show conflicting results. For instance, Cutting (1978) reported anosognosia in 87% after right and 54% after left hemisphere damage. By contrast, an incidence of 62% in patients with right-sided damage and 67% in left-sided damage was found in a different study (Celesia et al., 1997). A direct comparison between these two studies is not without problems, though,

because the former investigated the attitude towards the paralysed side of the body whereas the latter investigated hemianopic anosognosia.

Many explanations for anosognosia have been put forward, including the concept of a denial mechanism (Weinstein & Kahn, 1955), the idea of anosognosia as a body image disorder (Bogen, 1969; Galin, 1974; quoted by Cutting, 1978). Other approaches attribute anosognosia either to unilateral neglect or agnosia (Cutting, 1978) or the so-called 'discovery' theory (Levine, 1990). The discovery theory was based on the hypothesis that "the pathogenesis of anosognosia for hemiplegia may involve failure to discover paralysis because proprioceptive mechanisms that ordinarily inform an individual about the position and movement of limbs are damaged, and the patient, because of additional cognitive defects, lacks the capacity to make the necessary observations and inferences to diagnose the paralysis" (Levine et al., 1991, p.1770).

In this context, we focus on the relationship of anosognosia and unilateral neglect. Cutting (1978) concluded that unilateral neglect was not a significant factor in anosognosia but found a trend in the anosognosic patient group to show neglect behaviour. After analysis of the data, Levine et al. (1991) suggested that neglect might facilitate anosognosia but is not a necessary condition. Double dissociations between unilateral neglect and anosognosic left hemiplegia were reported by Bisiach et al. (1986b) and between neglect and bilateral hemianopic anosognosia by Celesia et al. (1997). To conclude, the data seem to suggest that anosognosia and neglect might be functionally unrelated.

3.1.6 Extinction

Sensory extinction may be defined as the failure to perceive and to respond to one of two simultaneously applied stimuli although each stimulus is detected correctly when presented on its own. Its relationship to unilateral neglect is a controversial issue. Because of its disputed nature the extinction phenomenon will be discussed fully after the different theories of neglect have been presented.

3.2. Information processing in unilateral neglect

3.2.1. The fate of the neglected stimulus and stimulus interactions

That the neglected stimulus in the contralesional field does not simply fall into oblivion has been demonstrated by Marshall and Halligan (1988). Their patient suffered from left-sided neglect. When the patient was presented two line drawings of a house, she judged them both as identical although the left side of one of the houses was on fire. However, in a forced choice task, the patient repeatedly preferred the non-burning house over the one in flames. Marshall and Halligan (1988) concluded that the behaviour of the patient suggested some influence of the neglected stimulus "upon cognitive functioning, albeit at some pre-attentional, pre-conscious level" (Marshall & Halligan, 1988, p.767). The experiment was repeated by Bisiach and Rusconi (1990) with four left neglect patients. The results were perplexing. Two out of four patients consistently preferred the burning house. The remaining two patients gave inconsistent responses. Even more surprising was that the tracing of the entire house which was in flames only alerted one patient to a difference: "Maybe there is something here. But what is it?" (Bisiach & Rusconi, 1990, p.645).

Similar results were reported by Young et al. (1992) in a single case study involving a left neglect patient. When the patient was presented with chimaeric objects, for example consisting of one half of a pig on the left side and of half a sauce pan on the right, she traced both the contours of the sauce pan and the pig correctly and then identified the object as a sauce pan. Even stranger was her reaction with chimaeric faces. If the examiners pointed to parts of the object on the left, the patient could describe them accurately, but she identified the chimaeric face as the right half-face in most of the cases. These reports have illustrated that although the neglect patient denies conscious awareness of neglected stimuli the processing of the stimuli interferes with the patient's actions and responses.

Mijovic-Prelec et al., (1994) tested a single patient in a combined detection and reaction time task. The target stimulus was a dot that appeared equally often left or right of a central fixation point. The patient was asked to respond verbally with either 'yes' or 'no' and to press a button simultaneously as quickly as possible. The patient responded with 'no' in two conditions: When the dot appeared in the contralesional

visual field and when the dot was not presented at all. However, the results showed that the patient made the 'no'-response much more quickly when the dot was present in the neglected visual field compared to the reaction times when it did not appear at all.

Facilitation effects mediated by neglected information have also been demonstrated in various studies using the semantic priming paradigm. For example, Làdavas et al. (1993) showed that a left neglect patient displayed an associative priming effect. When a target word shown in the right visual field was preceded by the short presentation of an associated word in the neglected visual field, reaction times were much faster to the target word (see also McGlinchey-Berroth et al., 1996). However, that "covert post-perceptual processing of neglected stimuli" (Làdavas et al., 1993, p.1307) does not exist in every neglect patients was shown by a study that examined context effects in neglect patients (Audet et al., 1991). Two left neglect patients were recruited for this study. Target stimuli were letters K or T which were projected on the right side of a computer screen. Three contextual conditions were created by flanking the target letter with either the same letter as the target (KK or TT, facilitating condition), by flanking the target letter with the letter O (OK or OT, neutral condition) or by flanking the target letter with the opposite target letter (TK or KT, inhibitory condition). The flanker always appeared to the left of the target in the horizontal condition or above the target in the vertical condition. No context effects were recorded when flanker and target appeared simultaneously but when the flanker preceded the target context effects emerged. This time both facilitatory and inhibitory effects were observed in the two patients, C.P. and A.A., for the vertical condition. In the horizontal condition, however, only C.P. displayed facilitation and no inhibition. Audet et al. (1991) concluded "considering the results of C.P., that the neglected item can be processed sufficiently to produce effects consistent with facilitation of the encoding mechanism but not to the level where a decision and a response are made. The difference between the results obtained for A.A. and C.P. reflects a discrepancy in the level of processing attained by the neglected item. Since these two patients also show a difference in the magnitude of their visual neglect, as revealed by our initial assessment, it seems that the nature of processing in the

neglected field may be dependent on the severity of the disorder" (Audet et al., 1991, p.21).

To conclude, although neglected stimuli are not perceived consciously, they do interfere with the processing of the stimulus presented to the non-neglected field. This potential interference may not emerge, though, if neglect is severe. In the next section, we will look at conditions that improve conscious processing of stimuli in the impaired hemifield.

3.2.2. Cueing effects

There has been controversy in the discussion of cueing, i.e. the attempt to shift visuo-spatial attention to the neglected side. For example, Heilman and Valenstein (1979) dismissed positive cueing effects a priori. Their hypothesis was that unilateral neglect is caused by a hypokinetic/hypo-aroused right hemisphere (see below for detailed discussion). Therefore, attracting attention to the left should not influence "any act that must be performed in the neglected field" (Heilman & Valenstein, 1979, p.166). In this study, six patients with left neglect performed a modified line bisection task with letters on either end of the line. Before they marked the midpoint, they were asked to name a letter on either the left or the right side of the line. Heilman and Valenstein (1979) reported that reading the letter on the left did not alter the performance in relation to a right-sided letter position.

In contrast, Riddoch and Humphreys (1983) questioned this result and hypothesised that no cueing occurred due to the competing stimulus in the non-neglected field. Heilman and Valenstein's (1979) paradigm was extended in their study and five left neglect patients were tested on four cueing conditions: (a) no cue present, (b) a single left cue present, (c) a single right cue present, (d) both left and right cues present. The results showed a significant improvement of neglect when patients were forced to name a stimulus in the neglected field. Unlike in Heilman and Valenstein's (1979) study, this was the case even when a competing stimulus was present in the non-neglected field.

Halligan and Marshall (1989b) designed a modified line bisection paradigm to remedy one of the reasons why Heilman and Valenstein (1979) might conceivably have failed to demonstrate a positive cueing effect, namely that the cue-task ("name

letter") is not connected with the experimental task (line bisection). Therefore, a line bisection task was constructed that involved moving a cursor arrow by operating a mouse which lay in the patient's ipsilesional, i.e. right hand to bisect a line displayed on a computer screen. Cueing was achieved by having the cursor in the initial position at either the left or the right end of the stimulus line. The results showed that starting the cursor on the left end of the line to be bisected lead to a significant reduction of neglect.

A related form of the above 'sensory' cueing was proposed by Halligan et al. (1991) who termed it spatio-motor cueing. Halligan et al. (1991) compared the performance of a patient in a line bisection task using his right and left hand in the right and left hemispaces. In the 'natural' position, the left hand started on the left side of the line and the right hand on the right side. In the 'unnatural' position, the hands crossed over into the opposite hemispace. Deviation to the right side was ameliorated when both the left and the right hand were placed at the left end of the line which was subsequently bisected by the patient starting from this position. By contrast, when the left hand bisected the line from the right end, neglect was slightly worse compared to when the right hand was positioned to the right of the line. Halligan et al. (1991) suggested that the left or the right hand functioned as a spatial cue and that right hemisphere activation was not the main factor in improving the performance (see also Robertson & North, 1992; Robertson et al., 1992).

Other studies have demonstrated 'panoramic' cueing where the shape of the ground (Halligan & Marshall, 1995) and the shape and size of the object to be bisected (Marshall & Halligan, 1991; Tégner & Levander, 1991; Halligan & Marshall, 1991b, 1994) can interfere with neglect behaviour.

Weintraub and Mesulam (1988) demonstrated that the organisation of a stimulus array can influence the performance of left neglect patients in a visual target cancellation task. When the array was structured, a more systematic and efficient search pattern was performed. Similarly, in a study by Kartsounis and Warrington (1989), neglect deficits were almost abolished when the stimuli were continuous. Another factor that decreased neglect scores was the meaningfulness of the stimuli for example in a picture showing two interacting figures in comparison to a picture depicting a number of unrelated objects.

Mattingley et al. (1994) demonstrated a cueing effect of slowly drifting background motion. Lines were bisected much more accurately by left neglect patients when a random dot background was displayed simultaneously that moved slowly towards the left.

Brunn and Farah (1991) achieved an improvement in the performance of eight right hemisphere damage patients through manipulation of lexical parameters. The patients were presented with words and non-words. Each letter string was underlined by a line of the same length as the word/non-word. It was demonstrated that lexicality had a marked effect on the line bisection performance by shifting attention to the left. Accuracy was best when lines under words had to be bisected.

Bisiach et al. (1981) reported successful "internal" cueing. The study is an extension of their influential Milan cathedral square paradigm (Bisiach & Luzatti, 1978). First, the patients were asked to imagine themselves standing on the opposite sites of the square, describing the objects in the square for each position. In the second part of this experiment, however, the patients were asked to describe the right and then the left side of the square in relation to the first position and then the left and the right side of the square according to the second perspective. Bisiach et al. (1981) showed that the patients with unilateral neglect reacted to the cued condition, and their description of internal visual representations improved significantly.

To conclude, cueing is a phenomenon that has been established in many studies although it might not be effective in every patient. In the next section, theories of unilateral neglect will be presented. More specific clinical aspects of neglect will be addressed to illustrate the various accounts.

4. Theories of unilateral neglect

In this section, we will give an overview of the different approaches to neglect. Different theories will be discussed that have located neglect on a sensory, perceptual, representational, attentional and intentional level.

4.1. Neglect as a sensory impairment

A strong association of visual field loss and neglect has repeatedly been reported. Celesia et al. (1997) observed that in a sample of 32 hemianopic patients 72% of the subjects displayed symptoms of unilateral neglect. A study by Hecaen (1962; quoted by Riddoch & Humphreys, 1987) produced a similar figure. According to Hecaen (1962), 76% of neglect patients suffered from hemianopia. Battersby et al. (1956) surveyed a group of 122 brain damaged subjects and found that all of their 41 neglect patients had visual field defects. Based on these results, Battersby et al. (1956) proposed an account that considers unilateral neglect as the consequence of defective sensory input, mainly in the visual modality, which is "superimposed upon a background of altered mental functioning" (Battersby et al., 1956, p.92; see also Sprague et al., 1961). Zarit and Kahn (1974) examined a group of 89 unilateral brain damaged patients and discovered that visual field defects had the largest association with the patients' neglect scores. However, 27 patients with low to moderate neglect scores did not have any visual defects at all. Zarit and Kahn (1974) concluded that the amount of neglect was "related to the total severity of all deficits, rather than to one specific dysfunction" (Zarit & Kahn, 1974, p.63).

By contrast, Albert (1973) demonstrated a clear dissociation between neglect and visual field deficits. In the left hemisphere group, only ten percent of the neglect patients had visual field defects and only 17% of patients with visual field defects suffered from neglect. On the other hand, in the right hemisphere group 50% of patients who had visual field defects showed visual neglect and only 55% of neglect patients had visual field defects. In addition, Halligan et al. (1990) reported that even if neglect and visual field deficits coincide, neglect is not exacerbated by a visual field defect. Furthermore, Vallar et al. (1991) compared the response pattern of evoked potentials in two left and right hemisphere patient groups. All patients involved in the study had been diagnosed as suffering from hemianopia. One group also displayed neglect symptoms whereas the other subject group did not have any other impairment. The visual evoked potentials after visual stimulation in the intact field were normal for both groups. By contrast, no cortical evoked response was recorded to contralesional visual stimuli in the non-neglect group, whereas the neglect patients showed normal evoked potentials to stimuli presented to their

neglected half-field. Vallar et al. (1991) concluded that the inability to perceive a stimulus is not likely to be due to a primary sensory deficit.

Vallar et al.'s study (1991) also demonstrated a further problem concerning the diagnosis of neglect and hemianopia, namely that the former can masquerade as the latter. The traditional clinical confrontation and perimetry techniques to diagnose neglect and visual field defects are often not refined enough to disentangle the two (for a more specific test see Meienberg, 1983). Kooistra and Heilman (1989) illustrated these difficulties in a single case study. Their patient who suffered from unilateral neglect appeared to have a left visual field defect on confrontation testing. However, when the patient directed the eyes to the right hemispace, the detection of the stimuli that were presented to the supposedly hemianopic field located in the right hemispace improved significantly. This drop of error rates would have been impossible if the defect had been a purely sensory one. A similar improvement in the performance of a supposed hemianopic neglect patient was achieved by slightly modifying the set-up of a detection task (Walker et al., 1991). Simply by introducing a delay of 100 ms after the central fixation point had disappeared from the screen and before the presentation of the target reduced the severity of neglect and abolished the symptoms of an apparent hemianopia. These examples indicate that the presence and importance of hemianopia in neglect patients might have been overestimated in the studies that reported a strong correlation.

Further evidence for the view that there is no relationship between neglect and visual field defects comes for example from Bisiach and Luzzatti's study (1978). Two left brain damaged patients persistently neglected left-sided details in imagined pictures independent of perspective. This behaviour demonstrated that neglect can be found in tasks that do not require visual input. Also, sensory theories cannot account for the fact that some patients show neglect in the ipsilesional hemispace (Weintraub & Mesulam, 1987), for positive cueing effects (e.g. Riddoch & Humphreys, 1983; Robertson, 1989; Kartsounis & Warrington, 1989), for dissociations in difference reference frames (Halligan and Marshall, 1991c; Beschin et al., 1996) or for a higher incidence of neglect after right hemisphere damage (e.g Brain, 1941; Critchley, 1950).

A different aspect is the question whether an impairment of visual scanning underlies or contributes to neglect (Denny-Brown & Fischer, 1976). Deviation of the gaze to the ipsilesional space is a typical feature in neglect patients although the patients are generally able to move their eyes to the contralesional field on command. Girotti et al. (1983) studied the saccades of 22 patients with right and left hemisphere damage. Seven subjects, all with right hemisphere lesions, were classified as neglect patients. The subjects in Girotti et al.'s study (1983) were required to keep their eyes fixed on a central target and to move the gaze as quickly as possible when a visual target appeared on the screen. The saccadic eye movements of the neglect patients were characterised by the following behaviours: No eye movement was initiated to 25% of left peripheral targets, the reaction time was increased and there was also a staircase pattern in the left hemifield. Furthermore, the oculo-motor disturbances of neglect patients were independent of an intact visual field. Ishiai et al. (1987b) examined the eye fixation patterns of 25 patients with unilateral brain damage. The subjects' fixation points were recorded while viewing simple geometrical figures (a horizontal line and a line drawing of a rectangle). While hemianopic patients without neglect compensated for their visual field deficit by looking at the impaired side longer, the neglect patients did not apply any compensatory strategies (see also Chatterjee et al., 1992; Karnath & Huber, 1992).

The comparison between hemianopic patients without neglect and neglect patients seems to indicate that degraded visual information is not the underlying reason for the neglect patients' oculo-motor pathology. Hornak's study (1992) supported this view. The eye movements of five right hemisphere neglect patients were recorded as they searched in a completely darkened room for any target lights. This paradigm was chosen to remove a scanning bias to the ipsilesional side caused by the "attraction" of more complete sensory information. The results showed that fixations nevertheless were directed almost entirely to the right of the midline. A control group with visual field defects, though, searched equally to both sides. In other words, neglect patients do not look to the contralesional side because they do not perceive much there. The altered oculo-motor behaviour seems to be caused by a more high level mechanism.

However, oculo-motor deficits alone cannot account for neglect of imagined representations (Bisiach & Luzzatti, 1978). Also, Posner et al. (1984) have demonstrated neglect in visual tasks that were not accomplished through eye movement.

As for the relationship of neglect and sensory impairment in other modalities than vision, the data point towards the same conclusion. Vallar et al. (1991) compared somato-sensory evoked potentials (SEPs) in two groups of patients who had all been diagnosed as suffering from hemianaesthesia. One group had been classified as neglect patients, the other did not show signs of neglect. Neglect was assessed with visual exploratory tasks. Whereas the SEPs to stimuli to the ipsilesional hand were normal in both groups, the non-neglect group did not show any cortical evoked responses to stimulation of the contralesional hand. By contrast, the neglect group had normal SEPs independent of the side of somato-sensory stimulation indicating that the diagnosed hemianaesthesia was a symptom of neglect rather than of a primary sensory deficit (see also Vallar et al., 1991b). Similarly, Bisiach et al. (1984) tested 107 unilateral brain damaged patients with regard to auditory lateralisation. Fifteen patients were classified as visual left neglect patients. An impairment of auditory lateralisation, i.e. a systematic directional error towards the ipsilesional side, was considered a symptom of neglect caused by a distortion of the internal representation of egocentric space (Bisiach et al., 1984). Although the results were not significant, the visual neglect patients showed a greater mean standard deviation error than the right hemisphere patients without neglect. However, pure tone audiometry did not reveal any sensory impairment in any of the patients including the neglect group. In a different study, De Renzi et al. (1989) examined auditory and visual neglect patients and did not find any difference in auditory threshold between ears, either.

In conclusion, a theory that seeks to explain neglect as a sensory impairment does not do justice to the abundance of data against this position.

4.2. Neglect as a perceptual impairment

Denny-Brown et al. (1952) proposed a theory of neglect (and extinction) that located the impairment on a perceptual rather than a sensory level. A detailed single case study described the case of an elderly lady who probably had suffered infarction of the right parietal lobe. The diagnosis was based on clinical observation. The patient showed signs of tactile and visual extinction. She also displayed clinical signs of left spatial neglect. For example, she had massive difficulties dressing her left side, kept getting lost in the ward although her mental status was relatively unimpaired, omitted objects on the left when asked to draw or to describe a scene and had problems reading because she started in the middle of each line. According to Denny-Brown et al. (1952) the function of the elementary senses of touch, pain and temperature were preserved. "If a touch with one hair is not perceived at all, but of six hairs perceived one time in ten, it can also be assumed that the very light touch with one hair set up normal sensory conduction". "We must therefore distinguish between sensory conduction and perception" (Denny-Brown et al., 1952, p.453). It was further proposed that neglect is caused "by an inability to reach a conclusion regarding the origin of multiple sensory data" (Denny-Brown et al., 1952, p.452). In this framework, the parietal cortex has the function of spatial summation, of integration of multiple sensory information and the recognition of form, a process which Denny-Brown et al. (1952) termed 'morphosynthesis'. Accordingly, neglect reflects an impairment of this normal function ('amorphosynthesis'). When the generation of a distinct perceptual representation is insufficient, this weak representation will be "eliminated in rivalry with those better perceived" (Denny-Brown et al., 1952, p.469). Unilateral damage will therefore lead to neglect symptoms in the contralesional hemispace. Denny-Brown et al. (1952) observed altered attentional behaviour of the patient, but the changes in the ability to allocate attention were regarded as an epiphenomon by the authors.

Since Denny-Brown et al.'s publication (1952), it has clearly been shown that neglect can occur after damage to cerebral areas other than the parietal cortex (Vallar & Perani, 1987). Also, the amorphosynthesis theory cannot account for ipsilesional neglect (Weintraub & Mesulam, 1987) and dissociations between modalities or within various reference frames (Halligan and Marshall, 1991c; Beschin et al., 1996).

Bisiach and Vallar (1988) criticised the amorphosynthesis model on various accounts. Firstly, it is pointed out that the amorphosynthesis theory does not explain the strong association of neglect and right hemisphere damage. However, as Marshall et al. (1993) rightly stressed, Bisiach who is one of the main advocates of a representational account of neglect did not incorporate explanations regarding hemispheric asymmetries in his theory either (Bisiach & Luzzati, 1978; Bisiach et al., 1979). Secondly, the amorphosynthesis theory cannot "be offered as a basic explanation of the syndrome at issue. ... Evidence of neglect phenomena in the domain of mental representation has started to accumulate. Therefore, these phenomena can no longer be reduced to disorders affecting the collection and processing of external stimuli, i.e. to disorders which only involve the sensorimotor processing of spatial information via external loops" (Bisiach & Vallar, 1988, p.207). This line of argument is not convincing. It has not been established to what extent higher mental processes build on fundamental perceptual representations. They might be inextricably entwined with each other. For example, within the framework of the temporal correlation hypothesis (Singer & Gray, 1995), Singer (1994) linked attentional processes with fundamental mechanisms of perception on a neurophysiological level. An impairment on a perceptual level could therefore account for at least some neglect phenomena.

4.3 Neglect as a representational impairment

One of the earliest accounts that falls into the representational category was a theory put forward by Zingerle (Zingerle, 1913; quoted by Bisiach & Berti, 1987). In this publication, neglect was understood as a disorder of the conscious representation of one side of the body and of extra-corporeal space. Later work that associated neglect with disturbances of the body schema (e.g. Brain, 1941; Gerstman, 1942; Lhermitte, 1942; Roth, 1949; quoted by Bisiach & Vallar, 1988) has been considered "an embryonic representational account" (Bisiach & Vallar, 1988, p.211). "Visual localization is ... a process involving the body scheme and the scheme of the external world" (Brain, 1941, p.263).

More recently, Bisiach and his colleagues have developed this concept of an altered representational space extensively (Bisiach & Luzzatti, 1978; Bisiach et al., 1979;

Bisiach et al., 1981; Bisiach et al., 1984; Bisiach et al., 1985; Bisiach & Berti, 1987; Bisiach & Vallar, 1988; Bisiach et al., 1994; Bisiach et al., 1996). First evidence for the definition of unilateral neglect as a distorted internal representation of space came from a study that demonstrated neglect behaviour in mental images. In this study, Bisiach and Luzzati (1978) examined two patients following right hemisphere damage with both neglect symptoms and right-sided hemianopia. The patients were required to describe the Piazza del Duomo in Milan, in one condition as if they were facing the front of the cathedral and in the other as if they had the cathedral behind them, i.e. facing the place from the other side. The place had the advantage that it was very familiar to the patients, that it had a square shape and that it had roughly the same number of prominent features on each side. The results demonstrated that the two patients significantly neglected objects on the left side of the place, in both conditions. Similar results were obtained in an investigation where left neglect patients failed to access left hemispatial memories, independent of perspective (Meador et al., 1987; 'left' means the left side from two opposite vantage points on different trials). In a different study (Bisiach et al., 1981), Bisiach and his colleagues extended their above experiment (Bisiach & Luzzatti, 1978). The control group comprised 41 non-neurological patients. A group of right brain damaged patients was further subdivided into four groups: Twelve patients without hemianopia and neglect (-H, -N), ten patients with hemianopia but without neglect (+H, -N), 15 patients with both hemianopia and neglect (+H, +N) and finally a group of patients classified as a misplacement group. The latter group committed misplacement errors unrelated to the details of the square and was therefore excluded from a comparison with the other three groups. The first experiment in this study was a complete replication of the one described in Bisiach and Luzzati (1978). The results showed that the +H +N group significantly omitted details on the left side of the descriptions, thereby confirming the results obtained in Bisiach and Luzatti (1978). However, in the second part, spatial constraints were introduced. The patients were asked to describe the right and then the left side of the square according to the first perspective, and then the left and the right side according to the second perspective. Interestingly, in this cued condition, only the +H +N group produced a significant result in that their performance on the left side of the square improved considerably. A study on

mentally reconstructed images (Bisiach et al., 1979) provided further evidence in support of the proposed representational account. Thirty non-neurological control patients and 19 right brain damaged subjects performed a same/different judgement task on pairs of cloud-like shapes presented to them on a projector screen in the static condition. Each object was shown one at a time. In the dynamic condition, only a partial view of the shapes was permitted through a slit in the middle of the screen. The objects were moving one after the other either from left to right or from right to left. Through this technique, "a translation from an objective temporal dimension into a representational spatial one" (Bisiach et al., 1979, p.615) was required. In both conditions, the brain damaged group had marked difficulties in detecting differences on the left side of the shapes. Also, rightward movement in the second part did produce an improvement through a recency effect but there was still an overall left/right gradient in the performance of the brain damaged group.

Ogden (1985) used the same experimental paradigm and replicated Bisiach et al.'s findings (1979). The only difference was the inclusion of left hemisphere neglect patients who also showed contralesional neglect in constructed visual images. Further support for a representational account was provided by Barbut and Gazzaniga (1987). They presented a left neglect patient who displayed signs of disturbances in the conceptual space that involved language processes. In an oral spelling test, he displayed an increase of error rates at the beginning of words. In spontaneous speech, he often omitted the left side of the word. For example he was reported to say "portant" instead of "important".

To explain the above findings, Bisiach and his colleagues have subscribed to a view that claims analogue processes in the generation of mental images and spatial representation (Bisiach et al., 1985). The camp in favour of the analogue position is for example represented by Kosslyn (1981) as opposed to Pylyshyn (1981) who is a proponent of the propositional approach to mental imagery. In the former account, images are generated when a quasi-pictorial image is created in a visual buffer on the basis of information stored in long-term memory. In contrast, according to Pylyshyn's view (1981), "the imagery data are produced when subjects consider (without making use of analogue images) what something would look like if they were actually seeing it as it typically appears" (Kosslyn, 1981, p.62).

Accordingly, Bisiach and colleagues (1981) have argued that the representation of an object is isomorphic and that the imaginal space is organised in a topological structure across the two hemispheres. It was suggested that neglect is caused by an impairment of the contralesional half of the spatial framework of visual representation (Bisiach et al., 1981). The structure of the altered spatial framework was further specified by Bisiach et al. (1996). Bisiach et al. (1996) replicated the findings in a modified line bisection task of a previous study (Bisiach et al., 1994). It was found that left neglect patients when asked to mark the endpoints of an imaginary horizontal line of a given length on the basis of its midpoint printed on a sheet of paper misplaced the endpoints left wards. This observation is surprising as oculo-motor studies have demonstrated that neglect patients hardly, if at all, scan the contralesional space (e.g. Ishai et al., 1987, 1989; Hornak, 1992). Bisiach et al. (1996) interpreted their results as evidence for an anisometry of the horizontal space. According to this view, the organisational principle is a logarithmic scale with compression of the ipsilesional and expansion on the contralesional side. However, it is not clear why Halligan and Marshall's (1991) theory was discarded as an acceptable explanation for the data. Halligan and Marshall (1991) proposed compression of the contralesional space towards the ipsilesional space as one of the underlying mechanism in unilateral neglect.

Furthermore, the validity of analogue theories of mental images has been corroded by the findings of Guariglia et al. (1993). In a single case study, a left neglect patient was presented who displayed left neglect in visual imagery but no neglect symptoms either in the personal, peri- or extra-personal space. This result called into question the view that vision and visual imagery are based on the same mechanisms.

Also, as Bisiach and Rusconi (1990) pointed out themselves, the impairment of reconstructing the left side of visual images might have been caused by an inability to scan the picture through the central vertical slit rather than a representational distortion. A further shortcoming of the theory is the inability to explain neglect in the ipsilesional field (Weintraub & Mesulam, 1987), dissociations of any kind (e.g. Halligan & Marshall, 1991c; Beschin et al., 1996) or a left/right gradient in the performance of neglect patients within the ipsilesional field (De Renzi et al., 1993; Làdavas et al., 1990). Similarly, no mention is made why neglect should be more

frequent after right-sided lesions (e.g Brain, 1941; Critchley, 1950). Another aspect of neglect that the representational theory cannot account for is cueing (e.g. Riddoch & Humphreys, 1983; Robertson, 1989; Kartsounis & Warrington, 1989). Positive cueing effects are incompatible with the concept of a disrupted imaginal space and rather point towards a disorder of an attentional nature.

A second theory within the representational framework placed the disruptions of mental imagery at the level of working memory for visual and spatial information (Ellis et al., 1996). "It seems clear that working memory for the contralesional hemifield is not activated in neglect patients, and therefore, neither is there activation of a working memory representation for incoming information in the affected field nor for motoric feedback from movements to parts of the stimulus in the neglected field" (Ellis et al., 1996, p.77). It seems clear, though, that the shortcomings of Bisiach's representational theory apply in the same way to the spatial working memory model.

In summary, although the representational approach might capture some of the symptoms in neglect patients well, the account will always remain metaphorical and descriptive. In the next section, we will discuss theories that tackle neglect from an attentional vantage point.

4.4. Attentional theories

We will mention four attentional approaches that have been proposed to explain unilateral neglect: (1) Posner's disengagement theory (Posner et al., 1984; Posner & Raichle, 1994), (2) Heilman's hemispace model (Heilman & Valenstein, 1972; Watson et al., 1973; Heilman et al., 1993), (3) Kinsbourne's orientational bias theory (1970, 1970b, 1977, 1987, 1993) and, finally, Halligan and Marshall's panoramic versus focal processing approach (Halligan & Marshall, 1994; Marshall & Halligan, 1994).

4.4.1. Neglect as an impairment to disengage attention

Posner et al. (1984) tested six right and seven left hemisphere patients. In all patients the parietal lobe was involved. Signs of neglect were not a compulsory inclusion

criterion. However, eight patients displayed symptoms of neglect ranging from minimal (extinction behaviour) to moderate contralesional neglect ("neglect disables patients in most activities of daily living"). The neurological control group included three patients with frontal lobe lesion and two subjects after temporal lobectomy due to intractable epileptic seizures. No mention was made whether the control patients were tested for any signs of neglect. The basic experimental paradigm was a reaction time task in which the subjects were required to report a target stimulus on a computer screen. Before the target appeared, a cue was displayed that attracted the subject's attention either to the target position (valid trial) or to some other location on the screen (invalid trial). Posner et al. (1984) postulated three basic mental processes in shifting covert attention: Disengaging from the current focus of attention, moving to the new target and engaging the new target. It was further claimed that in the above paradigm conclusions regarding the disengagement operation can be made although it is not possible to monitor disengagement directly. An indirect measure of the disengagement operation was the comparison of the reaction times in the invalid trial (attention was engaged elsewhere) and the valid trial condition (attention was engaged in the correct location). Shifting and engaging attention was tested in the valid trial condition. The results demonstrated that the parietal group was equally efficient to react to targets after a valid cue irrespective of the side of presentation whereas response normally tends to be faster to ipsilesional targets and slower to contralesional targets when no clue preceded the target (Posner & Raichle, 1994). In contrast, a marked difference between reaction times to ipsilesional and contralesional targets emerged in the invalid trial condition. Reaction times were greatly increased to contralesional targets after an invalid cue had been presented in the ipsilesional hemispace. This effect was more marked in the right hemisphere group but the patients with left-sided parietal lesions had significantly increased reaction times to contralesional targets, too. No difference arose in the control group. Posner et al. (1984) concluded that first there was an asymmetry in the control of attentional orienting that favours the right side and, second, after parietal injury one specific operation in covert orienting, namely the disengage operation, was impaired. The authors consequently proposed this deficit as one of the underlying mechanisms in neglect patients.

Posner and Raichle (1994) acknowledged that neglect may arise from lesion sites other than the parietal lobe but focused on the parietal area "because lesions of the right parietal lobe lead most frequently to neglect" (Posner & Raichle, 1994, p.157). The disengagement theory, though, cannot account for the results in a modified line cancellation task provided in a study by Mark et al. (1988). The patient group consisted of ten right hemisphere subjects. In seven patients out of the ten, the parietal lobe had been damaged. Two versions of Albert's (1973) line cancellation task were performed by the subjects. In one task, the patient was asked to draw over each of the 40 red lines with a black "dry erase" marking pen as completely as possible. In the second task, the patient was instructed to erase each line using a small sponge. The difference between the two tasks was that in the former the cancelled out lines were left in place whereas in the latter version the lines were removed. Mark et al. (1988) had set out to test the influence of stimuli in the non-neglected hemispace on the cancellation performance. Analysis of the results revealed that the performance improved dramatically when lines were wiped of the stimulus sheet which is predicted by the disengagement theory. However, the patients continued to neglect lines on the left, albeit fewer, in the sponge condition despite the fact that the right hemispace was largely empty. In other words, neglect persisted although there were hardly stimuli left in the ipsilesional hemifield the patients had to disengage attention from.

A similar behaviour was reported in a study involving two extinction patients who both had suffered damage to the right hemisphere which involved the parietal lobe (Rorden et al., 1997). The patients were asked to fixate on a central cross that was presented on a computer screen and to report on which side the stimulus had appeared first. Then, two horizontal bars were projected into each visual field. The bars could appear simultaneously on the screen, or they were presented offset to each other by an interstimulus interval ranging from 14 to 864 ms with the left bar appearing before the right in one condition and vice versa in the other condition. It was found that the left sided stimulus required a temporal lead of 200 ms to be perceived before the stimulus in the right visual field despite the fact that there was no ipsilesional stimulus that might have attracted the patients' attention.

Again, the disengagement theory cannot explain lateral differences in the incidence of neglect (e.g Brain, 1941; Critchley, 1950), the attentional gradient in the ipsilesional hemifield (De Renzi et al., 1993; Làdavas et al., 1990), the different dissociations (e.g. Halligan and Marshall, 1991c; Beschin et al., 1996) and neglect in the ipsilesional field (Weintraub & Mesulam, 1987). Cueing (e.g. Riddoch & Humphreys, 1983; Robertson, 1989; Kartsounis & Warrington, 1989) could be accounted for if one were to say that the attentional attraction of the cue in the contralesional hemifield is strong so that the neglect patient does not disengage from it to focus attention on an ipsilesional stimulus.

In summary, even if the disengagement theory described correctly some attentional mechanisms of the parietal lobe, it could only account for one of the many aspects of neglect behaviour after parietal injury.

4.4.2. Heilman's hemispace model

The following account defined unilateral neglect as an arousal disorder which is caused by disruptions of the cortico-limbic reticular formation network (Heilman & Valenstein, 1972; Watson et al., 1973; see also Mesulam, 1981). According to the model's more recent formulation (Heilman et al., 1993), unilateral neglect can be caused by unilateral lesion to the mesencephalic reticular activating system which normally inhibits the ipsilateral nucleus reticularis thereby controlling widespread activation of the whole cortex. A disinhibited nucleus reticularis decreases thalamic transmission of sensory input to the cortex. The multimodal association cortex sends activating collaterals to the mesencephalic reticular formation and inhibitory collaterals to the nucleus reticularis. Unilateral damage to the multimodal sensory convergence areas produce unilateral neglect because "the subject cannot be aroused to, or process, multimodal contralateral stimuli" (Heilman et al., 1993, p.299). In a dichotomous hemispace model, it was further assumed that each hemisphere contains its own activating system which orients attention to the contralateral hemisphere. Damage to one cerebral hemisphere will lead to an ipsilesional attentional bias. The attentional bias is caused by hypoactivity of the injured half of the brain (Heilman et

al., 1978) not by the disinhibited intact and hyperactive hemisphere as Kinsbourne (1987) has proposed.

To account for the higher incidence and more severe neglect symptoms after right hemisphere lesions it was postulated that the right hemisphere allocates attention to the left and right hemispaces. The left cerebral hemisphere is assumed only to deploy attention to the contralateral hemifield (Heilman & Van den Abell, 1980).

According to the model of Heilman and his associates, lateral attentional differences arise only between the two hemifields. This prediction was not borne out by studies which tested neglect patient on the deployment of visual attention within the ipsilesional field (Làdavas, 1987; De Renzi et al., 1989; Làdavas et al., 1990). De Renzi et al. (1989) tested eight right hemisphere neglect patients in a visual search task. Four letters where displayed to the right of a central fixation point. Left neglect patients displayed shortest response times when the target was presented at the rightmost position. The reaction times increased progressively as the target location was moved towards the centre. A similar result was reported by Làdavas (1987) and Làdavas et al. (1990) who showed that left neglect patients reacted most quickly to stimuli in a right relative position. These data, however, can be accomodated in Kinsbourne's attentional model of orientational bias (Kinsbourne, 1987, 1993) which will be presented in the next section.

Other critical points of this theory are a lack of explanatory power of the different dissociations (e.g. Halligan and Marshall, 1991c; Beschin et al., 1996) and neglect in the ipsilesional field (Weintraub & Mesulam, 1987). Cueing effects (e.g. Riddoch & Humphreys, 1983; Robertson, 1989; Kartsounis & Warrington, 1989), though, can be explained by postulating a strong enough attentional attraction exerted by the cue to activate the hypoaroused hemisphere.

4.4.3. Kinsbourne's orientational bias theory

Contrary to Heilman's model discussed above, Kinsbourne (1970, 1970b, 1977, 1987, 1993) proposed that neglect is a directional phenomenon. It is assumed that two antagonistic vectors, two opponent processors, which are reciprocally interactive direct attention to the contralateral sides of egocentric space. Neglect is the consequence of an imbalance between the processors. If one processor is impaired,

the other now disinhibited processor biases attention towards the opposite side of laterally extended space. The attentional gradient that follows from such a lesion extends across the entire egocentric space. The model also implies an attentional gradient within each hemifield, both within the contralesional and the ipsilesional hemispace and, therefore, predicts the phenomenon of ipsilesional neglect (Weintraub & Mesulam, 1987). Furthermore, the interaction between the processors occurs at multiple levels which can explain the multitude of lesions sites that cause neglect. To explain the greater incidence of left neglect, it was postulated that right and left directional tendencies, though opposite, are unequal. According to this theory, the left hemispheres generates a much stronger rightward turn than the right hemisphere to the left side.

Studies that have demonstrated an attentional bias towards ipsilesional stimuli within one hemifield provided support for the orientational bias model (Làdavas, 1987; De Renzi et al., 1989; Làdavas E. et al., 1990). Làdavas (1987) demonstrated further that the attentional gradient followed gravitational co-ordinates. Eight extinction patients with right hemisphere lesions were tested in a reaction time task. The subjects were asked to respond to visual stimuli that were presented in the left and right visual field. In one condition, the patients tilted the head either to the left or the right by 90 degrees and were required to respond to stimuli either above or on either side of a fixation mark. The data showed that in both conditions of head tilt the gravitational right stimulus precipitated faster responses than the gravitational left stimulus.

Another aspect of the model is the claim of unilateral vector enhancement due to selective activation of the contralateral hemisphere. Consequently, the prediction is that neglect is exacerbated or mitigated after stimulation of the intact or damaged hemisphere, respectively. The first case of transitory mitigation of neglect during vestibular stimulation was reported by Silberpfennig (1941; quoted by Kinsbourne, 1993). This observation has been replicated more recently (Rubens, 1985; Cappa et al., 1987; Vallar et al., 1993). Others have described mitigation of unilateral neglect and extinction symptoms through movement of the contralesional hand (Joanette et al., 1986; Robertson & North, 1992; Mattingley et al., 1998c; Halligan & Marshall, 1989c but see Halligan et al., 1991, for a different interpretation), left-sided transcutaneous electrical stimulation (Vallar et al., 1995) or through vibration of the

contralesional posterior neck muscles (Karnath et al., 1993). However, Robertson and North (1992) also reported that left finger movement was only effective in reducing neglect when it was performed in the left hemispace which is no concordant with Kinsboune's theory as it is predicted that left finger movement in the right hemispace improves neglect, too.

The concept of selective activation can also account for the baffling report on a single patient who displayed signs of crossed neglect symptoms (Costello & Warrington, 1987). A case of a patient was described who had sustained a left hemisphere lesion that extended into the right hemisphere. Interestingly, the patient showed right-sided neglect when copying simple geometric figures. However, he committed left-sided paralexic errors when presented with words. In other words, the hemispheric specialisation for a specific task determined to which side of the egocentric space the orientational bias was directed. However, the theory would also predict an improvement in line bisection tasks when the stimulus is presented in the contralesional visual field. This has not been borne out. Some studies found the opposite effect (Heilman & Valenstein, 1979; Ishiai et al., 1994) or no hemispace effect at all (Riddoch & Humphreys, 1983; Reuter-Lorenz & Posner, 1990). Also, like all of the other theories, the orientational bias model cannot account for dissociations in neglect (e.g. Halligan and Marshall, 1991c; Beschin et al., 1996).

In summary, Kinsbourne's orientational model is more flexible and dynamic than the theories discussed above and it succeeds in capturing many aspects of neglect behaviour.

4.4.4. Focal versus panoramic processing

In a number of studies, it has reliably been demonstrated that unilateral neglect patients do not fail in every task that examines spatial judgement. The configuration of the stimuli (Tegnér & Levander, 1991; Halligan & Marshall, 1991b, 1993b, 1994; Marshall & Halligan, 1991, 1994) and even the background (Halligan & Marshall, 1995) on which stimuli are presented have a modulatory effect on the judgement of spatial extent.

Marshall and Halligan's model is based on two assumptions: First, each hemisphere distributes attention in a contralateral direction with an attentional gradient (Kinsbourne, 1987; 1993) and second, the two hemispheres differ in the spatial scale they preferentially operate on. According to this view, the left hemisphere processes focal features of a stimulus array whereas the right hemisphere responds to stimulus properties on a global scale (Robertson & Delis, 1986; Delis et al., 1986; Robertson et al., 1988). Deployment of attention in the visual space has often been illustrated with the analogy of a 'spotlight'. The beam of an attentional 'spotlight' has three properties: (1) it moves from one area to the other, (2) "it moves in analogue fashion rather than jumping instantaneously from one location to another", (3) it possesses a specific size (Umiltà, 1988, p.175).

Jonides (1983) proposed a two-stage model of attentional selection according to which there are only two modes of allocating attention to a visual display: Attention can be spread evenly across the entire visual area or it can be focused on one small area of the visual array. By contrast, Eriksen and his colleagues put forward a model which incorporates an attentional spot light that can adjust its size according to the processing requirements. Therefore, the concept of a 'zoom lens' was proposed to describe attentional distribution more accurately (Eriksen & Yeh, 1985; Eriksen & St. James, 1986).

Combining the 'zoom lens' metaphor with hemispheric differences in spatial processing, Marshall and Halligan (1994) proposed that the left hemisphere might preferentially reduce the diameter of the attentional spotlight and the right hemisphere might increase its size. Based on these assumptions, right hemisphere damage should shift the orientational bias towards the extreme right hemispace. Furthermore, the processing mode of attentional distribution should be focal. This pathological processing pattern describes several of the symptoms of unilateral left neglect well. It was predicted that a task or a stimulus configuration which requires the deployment of panoramic/global attention should mitigate neglect symptoms. The prediction was borne out in several studies (Tegnér & Levander, 1991; Halligan & Marshall, 1991b, 1993b, 1994, 1995; Marshall & Halligan, 1991, 1994).

Tegnér and Levander (1991) examined 25 right hemisphere neglect patients in various bisection tasks. As predicted, long lines were bisected with a rightward error,

and the patients displayed a cross-over effect in the bisection of short lines, short paper strips and small circles. By contrast, large circles and long white paper strips were bisected either accurately, or with leftward error. A similar result was reported in a single case study involving a right hemisphere neglect patient (Halligan & Marshall, 1993b). The patient was perfectly able to mark the four corners of a stimulus page in a line cancellation task. However, he kept omitting lines on the left hand side irrespective whether his attention was drawn explicitly to the spatial dimensions of the stimulus sheet. In a different study (Halligan & Marshall, 1995), a modulatory effect of the stimulus sheet was indeed found. When horizontal lines were presented on differently shaped background sheets, the error decreased from rectangle-shaped to square- and circle-shaped background, respectively. In other studies (Halligan & Marshall, 1991b, 1994; Marshall & Halligan, 1991, 1994), it was demonstrated that accuracy in the bisection of squares and circles is far superior to the bisection of simple lines. Deviation decreased as the height of the figure increased. Furthermore, left neglect can be mitigated when the lines to be bisected form a square (Halligan & Marshall, 1994; Marshall & Halligan, 1994). The critical component for the accurate performance with squares seems to be a right vertical (Marshall & Halligan, 1994; Halligan & Marshall, 1994). The hypothesis that the patients might have used the estimated midpoint of a vertical to calculate the midpoint of the horizontal dimensions of the square was rejected on the grounds that no significant correlation was found between the vertical and horizontal displacements. It was therefore proposed that global attention processing was elicited by the configuration of the stimulus which "counteracts the (intact) left hemisphere's (intrinsic) tendency to orient rightwards with the subsequent 'capture' of focal attention by that part of the stimulus array which is in the extreme right position" (Halligan & Marshall, 1994, p.20).

It was further suggested that the global amelioration effect was mediated by the left intact hemisphere. The effectiveness of a vertical in the right hemispace might have prevented the left hemisphere from narrowing its 'zoom lens' (Halligan & Marshall, 1994). An analogy to simultanagnosia was drawn (Halligan & Marshall, 1993b). Whereas classic simultanagnostic patients are able to perceive only one object at a time even if two overlapping objects are directly projected into foveal vision,

unilateral neglect was regarded as "a form of lateralized simultanagnosia for objects represented at a 'small' spatial scale" (Halligan & Marshall, 1993b, p.172). Even when the neglect patients trace the silhouette of an object with two components (e.g. chimaeric object or flowers in flowerpot), they fail to perceive consciously the contralesional component (Bisiach & Rusconi, 1990; Young et al., 1992).

A related account for simultanagnosia was presented by Thaiss and De Bleser (1992). In a single case study, a subject suffering from simultanagnosia secondary to presenile dementia was investigated for specific impairments in the patient's search strategies. It was proposed that the symptoms of simultanagnosia were due to the patient's inability to use global shape information. Amelioration of the symptoms was associated with decreasing size of the stimuli "thus suggesting that the disorder may be functionally localized to a reduction of the patient's attentional 'spotlight'" (Thais & De Bleser, 1992, p.620). After a literature review, the authors proposed further that disruptions at the two extreme ends of the attentional spectrum might cause symptoms of simultanagnosia. More precisely, a 'wide angle' attentional beam and a spotlight of narrow diameter can be selectively impaired with each of the deficits leading to simultanagnosia.

Although Marshall and Halligan (1994) restricted their model to left-sided neglect and considered it "less than fully formal and explicit" (Marshall & Halligan, 1994, p.516), the model could be extended to right neglect applying Thais and De Bleser's interpretation (1992). If a patient suffers a left hemisphere stroke, the focal processing abilities of the left hemisphere are impaired. The patient consequently has to resort to global and low resolution attentional strategies of object recognition. Precise focal processing of elements in the visual array would be affected. The attentional gradient exerted by the healthy right hemisphere would therefore lead to a shift to the extreme left side of the intact hemispace with the consequence of failure to integrate stimulus components on the right side of the visual array. Assuming that the attentional bias of the right hemisphere is less strong than the one of the left hemisphere, differences in frequency and severity of left and right neglect can be accounted for.

In summary, although phenomena like dissociations in neglect behaviour (e.g. Halligan and Marshall, 1991c; Beschin et al., 1996) cannot be explained in this framework, it offers important theoretical generalisations.

4.5. Directional hypokinesia

First proposed by Watson et al. (1978) and based on the hypoarousal model outlined above (Heilman & Valenstein, 1972; Watson et al., 1973; see also Fiorelli et al., 1991), directional hypokinesia refers to the reduced ability to act in the contralesional space or the reluctance to initiate and carry out movements towards the contralesional side independent of the side of the limb involved in such motor activities. Directional hypokinesia has to be separated strictly from the symptom of motor neglect which is defined as decreased utilisation of the contralesional body side without impairment of strength, reflexes and sensory function (see e.g. Laplane & Degos, 1983).

It has been suggested that each hemisphere is both involved in mediating attention and intention within the contralateral hemispace but also in mediating intention towards the contralateral hemispace (Heilman, 1987). That directional hypokinesia represents one aspect of unilateral neglect has been established in various studies. Heilman et al. (1985) demonstrated that right neglect patients initiated movements towards the contralesional side more slowly than towards the ipsilesional space. Coslett et al. (1990) tested four left neglect patients in a modified line bisection paradigm. Direct viewing was not possible and the stimulus array was instead projected on a monitor which could easily be moved in the two hemispaces. The directional hypokinesia model and an attention/representation account were under scrutiny. The former theory predicted that the bisection performance would be worse when the lines were bisected in the contralesional space whereas the side in which the monitor was presented would not matter. On the other hand, an attention/representation model would predict that the side of bisection was irrelevant whereas the side of display would determine the performance. More specifically, when the monitor was in the left hemispace, the deviation from the centre would be greater. Support for both theories was provided. Two patients behaved according to the predictions of the directional hypokinesia model and the other two patients

supported the attention/representation account. Comparable data were reported by Tegnér and Levander (1991b) who used a line cancellation task where direction of visual attention and of arm movement were decoupled. Four out of the 18 left neglect patients showed a clear hypokinetic behavioural pattern whereas ten patients behaved in accordance with an attention/representation model.

Stronger results in favour of the directional hypokinesia model were provided by Bisiach et al. (1990) who examined a group of left neglect patients in a modified line bisection experiment which uncoupled the direction of visual attention from that of hand movement. Thirteen out the 15 left neglect patients in the group showed leftward displacement due to the uncoupling and supported the predictions made by a hypokinesia model. However, Halligan and Marshall (1989b) used a similar uncoupling technique and found no motor component in the performance of the neglect patient.

Also concordant with the hypokinesia model are the results from Girotti et al. (1983) who examined oculo-motor behaviour in brain damaged patients. In the left neglect patients, absence of saccadic response to 25% of the targets, an increase in the reaction times and a staircase pattern in the left hemifield were documented. The absence of a cueing effect and an improved performance of line bisection when the line was bisected in the ipsilesional hemispace were interpreted as further evidence in favour of the directional hypokinesia model and against an attention/representation theory. The cueing stimulus was a letter at each end of the line. For half of the lines to be bisected the patients were instructed to look to the left of the line, to report whether he saw the letter and then to proceed with the bisection. For the second half of the lines, the same procedure was followed with the exception that this time the patient was asked to look to the right of the line (Heilman & Valenstein, 1979).

By contrast, Riddoch and Humphreys (1983) did not replicate the above results. A marked cueing effect using the same paradigm was found. Furthermore, in Riddoch and Humphrey's study (1983), the side of hemispace where the lines were bisected did not influence the results significantly. These data clearly demonstrated that there was no hypokinetic element in the neglect performance of the tested group. Similarly, Mijovic (1991) failed to find a significant effect of the direction of hand movement in a spatial exploration task performed by a group of left neglect patients.

The results of a single case study by Halligan and Marshall (1989) were also at odds with the predictions of directional hypokinesia. A patient with severe left unilateral neglect produced remarkably improved scores in a star cancellation and line bisection task when he used his left hand instead of his right one (see also Joanette et al., 1991). Also incompatible with the directional hypokinesia model were studies that reported modulatory effects on the performance of neglect patients elicited by stimuli and the background of the visual arrays (Halligan & Marshall, 1991b, 1993b, 1994, 1995; Marshall & Halligan, 1991, 1994; Tegnér & Levander, 1991).

However, studies that were unable to reveal hypokinetic behaviour in neglect patients do not necessarily disprove the existence of it. Support for this view came from work with neglect patients that reported dissociations between perceptual/sensory and exploratory/motor neglect (Bottini et al., 1992; Liu et al., 1992). Bottini et al. (1992) presented a single case study of a left neglect patient who showed abnormal exploration of the extrapersonal space when the task involved execution of movements in the contralesional hemispace using the right hand. To test the perceptual component of neglect, a Wundt-Jastrow illusion test was used which examines impaired perceptual analysis of the two hemispaces. In the latter test, the left neglect patient's performance was flawless. A double dissociation between directional hypokinesia and perceptual neglect was reported by Liu et al. (1992). Two neglect patients with right hemisphere lesions were examined. One of them showed extinction on double simultaneous stimulation in the visual, auditory and tactile modalities but performed almost normally in a spatial exploratory task. The second patient displayed the reversed picture of symptoms. One might argue that extinction is only a weak symptom of neglect and that the only slightly pathological performance in the exploratory task is not a surprising result. Therefore, this case might not reflect a true dissociation. However, the second patient represents a convincing case of dissociation between motor and perceptual components of neglect. In both studies (Bottini et al., 1992; Liu et al., 1992), the patients with directional hypokinesia had suffered damage to the frontal lobe. The association of a hypokinetic manifestation of neglect with frontal lobe damage has been suggested in Mesulam's cortical network theory (Mesulam, 1981). In later studies (Bisiach et al., 1990; Daffner et al., 1990; Tegnér & Levander, 1991), the role of anterior lesions for

motor aspects of unilateral neglect was further emphasised. However, recent work questioned the dichotomy frontal lobe lesion/motor neglect and parietal lesion/perceptual neglect (Mattingley et al., 1998). Six left neglect patients were tested of which three had suffered damage to the inferior parietal lobe and the remaining three neglect patients had a lesion in the inferior frontal lobe. It was shown that the parietal group had difficulties initiating leftward movements towards visual targets on the left side of space. No motor impairment was found in the group with anterior lesions.

In summary, the model of directional hypokinesia described an important element in the behaviour of neglect patients, even if a motor component cannot always be established. A word of criticism is required at this point. The authors of the directional hypokinesia theory have failed to specify how intention to execute a movement and attention are related as Rizzolatti and Camarda (1987) have done. To define failure of movement initiation simply as a "dysfunction of the systems necessary to activate motor neurons" (Heilman et al., 1993, p.282) is not satisfactory.

4.6. A pre-motor theory of spatial attention

Rizzolatti and Camarda (1987) proposed a model of spatial attention which was based on a series of circuits largely independent from each other. The motivation of this model was to account for the multiplicity and anatomical independence of cerebral lesions that can lead to neglect and "the congruence between attentional and motor deficits" after cerebral lesions (Rizzolatti & Camarda, 1987, p.309).
The model postulated a system where perception and motor planning are closely integrated to explain how attention is allocated in response to a stimulus or shifted actively towards a spatial sector. For example, when a stimulus is presented to a subject, a circuit of neurons is activated which plan action in space according to the stimulus location. The activation of this circuit and subsequent generation of a motor plan attracts attention towards the spatial co-ordinates where the motor plan will be implemented. On the other hand, active shift of attention is conceived of in the following way: "Since spatial attention is a consequence of the organization of motor plans in a spatial framework, the selection of a motor plan should automatically

produce a shift of attention toward the spatial sector where the action will be executed" (Rizzolatti & Camarda, 1987, p.308). In other words, if you want to shift attention to the left side of your body, plan a movement towards or in the left hemispace.

Unlike other models, the pre-motor theory has the great benefit of being able to account for dissociations of neglect between different sensory modalities (e.g. Bellas et al., 1988; De Renzi et al., 1989b; Guariglia et al., 1993) and different spatial co-ordinate systems like neglect in a three dimensional space and in personal-, peri- and extra-personal space (e.g. Bisiach et al., 1986; Rapcsak et al., 1988; Shelton et al., 1990; Halligan and Marshall, 1991b,c; Mennemeier et al., 1992; Beschin et al., 1996). Not clear however is the question of spatial representation within the egocentric and allocentric reference frames.

In the extended version of this theory, Rizzolati and Berti (1993) specified that not retinotopic but viewer-centred co-ordinates were used to code spatial information. This postulate, however, can not be reconciled with studies that have demonstrated environment-centred (Làdavas, 1987; Gazzaniga & Làdavas, 1987; Farah et al., 1990) and object-centred neglect (Driver et al., 1994). Previous interpretations of object-centred neglect (Driver & Halligan, 1991) were dismissed by Rizzolatti and Berti (1993, p.98): "The reported" object-centred "deficit implies a distinction between left and right, i.e. the sides of the objects as referred to the viewer. The deficit is therefore a special case of a *viewer-centred* representational deficit rather than an object-centred defect". Driver et al. (1994) met this criticism by choosing stimulus shapes with ambiguous axes that allowed manipulation of the location of target information in axis-based co-ordinates while target information was kept constant in egocentric co-ordinates. The results supported Driver and Halligan's (1991) interpretation that object-centred neglect can exist.

A further observation that did not fit into the premotor theory has been reported by Robertson and North (1992). A left neglect subject was investigated with regard to the beneficial effects of left arm movement. It was found that blind left hand movement in the left hemispace reduced neglect but not in the right hemispace although according to premotor theory attention to the left side of the body was activated.

An obvious point of criticism is the failure of the theory to accommodate dissociations between neglect in a sensory modality and the execution of movement due to neglect (Bottini et al., 1992; Liu et al., 1992). How can a patient have no deficits in a visuo-spatial task and deficits in an exploratory-motor task if spatial attention is determined by the organisation of motor plans?
Furthermore this theory fails to explain lateral differences in the incidence of neglect (e.g Brain, 1941; Critchley, 1950), the attentional gradient in the ipsilesional hemifield (De Renzi et al., 1993; Làdavas et al., 1990), and neglect in the ipsilesional field (Weinstein & Kahn, 1959; quoted by Kinsbourne, 1987).

In conclusion, the most important contribution of the pre-motor theory is the attempt to explain the different dissociations between modalities and reference frames that have been observed in neglect patients.

4.7. Neglect as a limited attentional/intentional capacity system of sequential processing

All the theories mentioned above strongly stress the lateralisation of the underlying pathological mechanisms. However, other studies have also suggested that there might be an impairment to attend to stimuli systematically irrespective of the hemispace (Robertson, 1989; Chatterjee et al., 1992).
Robertson (1989) examined a group of ten left neglect patients in a detection task. Two assumptions were made: First, there is a lateralised difficulty to attend to a stimulus and, second, there is also a general difficulty to deploy attention in space. Based on these premises, the prediction was made that under certain circumstances the latter condition can outweigh the former and neglect patients can be induced to commit more mistakes in the *ipsilesional* hemispace as opposed to the contralesional side. This prediction was confirmed, albeit not in every neglect patient. In the first experiment, the patients were required to detect and report stimuli that were either presented unilaterally or simultaneously on both sides of a computer screen. In a second experiment, a word which functioned as a cue appeared only on the left side in addition to the stimuli in the previous experiment. The task now was to read the word and, as before, to indicate the type and location of the non-linguistic stimuli.

The results showed that six of the ten left neglect patients committed most of their errors on the right hemispace when the presence of the word cued them towards the left side. Robertson (1989) consequently postulated the existence of a general difficulty in deploying attention across space.

Riddoch and Humphreys (1987) tested three left neglect patients in a search task and concluded that parallel processing was relatively preserved in the neglect group whereas serial processing was found to be abnormal which suggested that neglect might be associated with a pathologically reduced limited capacity system.

Chatterjee et al. (1992) provided further evidence for this conjecture. In a single case study, the visuo-spatial search patterns of a left neglect patient were investigated. In a cancellation task, the patient mainly followed a systematic and stereotypic vertical search pattern which was different from previous reports on search patterns (Weintraub & Mesulam, 1988). The extent of left neglect was not changed, although more horizontal movements were elicited, after foils had been placed in rows. The omission pattern was characterised by typical left-sided omission in both instances. In a third condition, the patient was explicitly instructed to cancel targets alternating to and from the right and left sides of the visual array. This time a different result emerged. More targets in the far right and far left were cancelled whereas the central area was neglected. In other words, cueing to the contralesional side did not change the extent of the neglect but altered the spatial distribution of the patient's neglect. Chatterjee et al. (1992) concluded that patient's behavioural patterns were characterised by "a limited capacity to sequentially be aware of or act upon the stimuli" (Chatterjee et al., 1992, p.657).

To conclude the above approach has addressed a further puzzling and important aspect of information processing in neglect. Therefore, to come a bit closer to an understanding of neglect, it seems wise to consider all the theories discussed as complementary to each other rather than on their own.

5. Recovery from unilateral neglect

The prognosis of recovery from neglect seems to be anchored to a crucial watershed period of around the first acute three months post-stroke when recovery reaches a

plateau (Stone et al., 1992). During these first three months there is a high probability of quick recovery particularly for left hemisphere patients. This contrasts strongly with the rate of remission of chronic neglect patients whereby left neglect patients seem to have the worse outlook again compared to right neglect (Robertson, 1993).

Hier et al. (1983) tested 41 patients with right-sided strokes. The first testing session took place within seven days of onset of stroke. The patients were re-examined at two- to four-week intervals until they recovered completely or were lost in the follow-up. Neglect was established in 46% of the patients as the failure to attend to left-sided visual and auditory stimuli. The recovery had a median duration of nine weeks and a 90% probability of recovery after 16 weeks. Unilateral spatial neglect on drawing was found in 85% of all patients. The median duration of recovery was eight weeks and after twelve weeks there was a 75% probability of recovery. Stone et al. (1991) examined a group of unilaterally brain damaged patients consisting of 18 right and 26 left hemisphere patients at three days and three months post-stroke. In one of the tests, a line cancellation test, 55% of right hemisphere patients compared to 42% of left hemisphere patients displayed neglect behaviour three days after the stroke. Three months later, all of the right neglect patients had recovered from neglect whereas it was still present in 33% of the left neglect patients.

It seems, however, that beyond the initial acute phase, the prognosis of recovery is not nearly as good and neglect symptoms can persist for years. Zoccolotti et al. (1989) examined 104 right brain damaged patients at a minimum of two months post-stroke. Only a slight trend for a negative correlation between time since stroke and severity of neglect was reported. A similar result was reported by Zarit and Kahn (1974) whose sample contained 19 left hemisphere and 52 right hemisphere patients. The patients were tested for neglect with a battery of different visuo-spatial tasks. The median duration post-stroke was three months but for some chronic neglect patients the time of onset of neglect reached back as far as twelve years. No correlation was found between neglect scores and time since onset of illness.

Denes et al. (1982) tested 24 left and 24 right hemisphere patients in a cross-copying task at a median duration of 50 and 57 days post-stroke respectively. The final assessment was six months later. Initially, neglect was diagnosed in 33% of the right hemisphere patients and in 21% of left hemisphere patients. Six months later, left

neglect was still present in 29% of the patients whereas none of the patients showed right neglect. Similarly, Robertson et al. (1990) diagnosed persisting left neglect after an additional six months in 73% of the patients who had shown neglect at a mean of 15 weeks post-stroke.

To summarise, recovery during the acute first three months is quick and mostly complete in left hemisphere patients. In a minority of left neglect patients, recovery is not complete and neglect persists. In the chronic phase, time since onset of neglect and recovery do not appear to be correlated.

6. Extinction

6.1. Introduction and definition

Several studies have reported a double dissociation between the phenomenon of extinction and neglect (e.g. De Renzi et al., 1984; Posner et al., 1984). Therefore, the question whether extinction and unilateral neglect are related disorders (e.g. Critchley, 1950; Denny-Brown et al., 1952; Friedland & Weinstein, 1977, Bender, 1977, quoted by Schwartz et al., 1979; Mesulam, 1981; Posner et al., 1984; Riddoch & Humphreys, 1987; Bisiach & Berti, 1987; Karnath, 1988; Bisiach, 1991; Heilman et al., 1993) or whether they should be regarded as independent phenomena (e.g. De Renzi et al., 1984; De Renzi et al., 1989b; Vallar et al., 1994; Weinstein, 1994; Di Pellegrino & De Renzi, 1995; Milner, 1995) has provoked some controversy in the literature.

Sensory extinction may be defined as the failure to perceive and to respond to one of two simultaneously applied stimuli although each stimulus is detected correctly when presented on its own. Usually, the extinguished stimulus refers to the stimulus that has been presented to the side contralesional to the lesion. De Renzi et al. (1984) reported that 47% of the patients with unilateral brain damage showed extinction for the stimulus in the contralesional hemifield. Only 5.5% of the patients extinguished the auditory ipsilesional stimulus on simultaneous bilateral presentation. According to De Renzi et al. (1984), ipsilesional extinction was only a partial and temporary result most of which disappeared after the first session. Also, a number of patients with ipsilesional extinction suffered from deterioration of their mental state.

However, Schwartz et al. (1979) reported that almost 20% of left hemisphere damaged patients suffered from ipsilesional extinction whereas less than one percent of the right hemisphere group extinguished the ipsilesional stimulus.

Loeb (1885; quoted by Bisiach 1991) and Oppenheimer (1885) were the first to report the extinction phenomenon in the tactile and auditory modality. A case of visual extinction was later documented by Poppelreuter (1917) which precipitated a number of studies on this subject (e.g. Holmes, 1918, 1919; Head, 1926; quoted by Critchley, 1949). A patient may suffer from multimodal extinction (e.g. Oppenheimer, 1885; Bender & Furlow, 1945; Bender & Cramer, 1948; quoted by Critchley, 1949; Nathan, 1946; Denny-Brown et al., 1952; Rapcsak et al., 1987; De Renzi et al., 1984; Di Pellegrino et al., 1995; Vallar et al., 1994) or from extinction that is restricted to one modality only (e.g. De Renzi et al., 1984; Vallar et al., 1994).

6.2. Incidence, severity and neuroanatomical substrates

De Renzi et al. (1984) investigated the incidence, severity and persistence of auditory and visual extinction in a large group of unilaterally brain damaged patients who were tested almost exclusively within the first three days of hospitalisation. The tests were repeated every three to five days until extinction could no longer be elicited on two consecutive sessions. The results showed that 46% of the 144 patients suffered from auditory extinction. After 30 days, auditory extinction was still present in 38% of the patients. One hundred and two patients were tested to investigate the relationship of visual to auditory extinction after excluding patients with visual field defects. Forty nine percent suffered from neither impairment, 19% of the patients displayed symptoms of auditory but not of visual extinction, 12.5% had impaired perception of bilaterally presented visual stimuli but no deficit in the auditory modality and, finally, four percent of the patients suffered from both visual and auditory extinction. From this it becomes obvious that severe symptoms of extinction in one modality do not necessarily involve other modalities.

These figures were replicated by Vallar et al. (1994) who tested their patients for visual and tactile extinction within 30 days of the cerebral trauma. Out of their group of 159 patients with unilateral brain damage, 71% had no extinction symptoms, 13% displayed signs of tactile extinction, 9% of the patients suffered from visual

extinction and 6% showed extinction symptoms both in the visual and tactile modality.

Much higher figures for the incidence of tactile extinction were reported in a study by Schwartz et al. (1979). Sixty four percent of patients out of a group of unilaterally brain damaged patients were diagnosed as suffering from extinction symptoms in the tactile modality.

While neglect appears to be much more frequent after right hemisphere damage, a comparable association does not seem to exist for extinction. Schwartz et al. (1979) examined 234 patients with unilateral cerebral damage. Extinction was associated with right hemisphere trauma in 70% of the cases compared to 59% after left hemisphere damage. The difference did not reach significance. A similar result was obtained by De Renzi et al. (1984). Fifty two percent of right hemisphere patients displayed signs of extinction and as many as 40% of the patients after left hemisphere damage extinguished one stimulus on bilateral presentation. Critchley (1949), too, observed a slightly higher, though not significantly higher, incidence of tactile extinction after right hemisphere damage. Vallar et al. (1994) analysed the site of lesion on CT scan with relation to extinction symptoms in their patients. The results deviated from the traditional view that extinction is mainly associated with parietal lesions (e.g. Critchley, 1949). Fifty two percent of the extinction patients had suffered damage to the deep structures of the brain. The most frequent lesion site in this group was the basal ganglia. Also included were the anterior peri-ventricular white matter, the posterior limb and the genu of the internal capsule. The remainder of the extinction group had suffered cortico-subcortical damage involving the peri-ventricular occipital white matter and the dorso-lateral frontal cortex most frequently. De Renzi et al. (1987) reported a similarly high association of deep structure damage and extinction. Forty percent of their visual extinction patients who displayed symptoms of extinction for more than 20 days had the site of lesion confined to the deep cerebral structures.

However, hemispheric lesions are not the only neuroanatomical correlate to cause extinction. Milner et al. (1968) reported a case of auditory extinction in a commissurotomised patient. Critchley (1949) quoted a case described by Bender (1945) where the patient who had suffered from a Brown-Séquard syndrome due to a

gun shot wound to the spinal chord displayed symptoms of tactile extinction. In the next section, we will deal with a more detailed presentation of characteristic extinction symptoms.

6.3. Clinical characteristics of extinction

Simultaneous presentation of two stimuli in two different hemispaces is not a necessary condition for the demonstration of extinction. Làdavas (1990) showed that in right hemisphere damaged patients speed and accuracy of response to horizontally aligned stimuli increased gradually from left to right. Feinberg et al. (1990) tested right and left hemisphere patients for tactile extinction. The two stimuli were applied simultaneously to body parts in the hemispace ipsilateral to the cerebral damage. Tactile extinction was found in both groups. The degree of extinction did not differ between the patients with left and right hemisphere damage. In a single case study, Di Pellegrino and De Renzi (1995) examined a right brain damaged patient with extinction. The patient was told to focus on a central fixation point. On unilateral left presentation of two visual stimuli, the patient extinguished the leftmost target stimulus in 41 out of 48 trials. The patient always reported both stimuli in the unilateral right condition. When the two stimuli were presented in two different visual fields, the left stimulus was extinguished in every trial.
Similar results were reported by Rapcsak et al. (1987) with regard to extinction of the leftmost stimulus on unilateral double presentation. In 80% of the trials the leftmost stimulus on unilateral left presentation was extinguished whereas in only three percent of the cases of right unilateral presentation the left stimulus was left unreported.

Evidence that extinction of a stimulus is not determined by the location within the visual field or by the position with respect to the head or trunk midline is provided by a different experiment in Di Pellegrino and De Renzi's study (1995). There were three conditions in a detection task. In condition 1, a central cross was projected onto the screen with two boxes, one on the left and one on the right side to the cross. Targets were presented either unilaterally or bilaterally. In condition 2 and 3, a dot appeared in the centre of the screen. Either to the left (condition 2) or the right of this

dot (condition 3), a cross flanked by two empty boxes was projected onto the screen (see figure1).

Fig. 1: Box display in condition 2.

The patient was asked to fixate on the central dot but to shift attention covertly to the cross and to report the number of targets appearing in the boxes. Either single or double targets were presented. The results showed the following patterns: In condition 1, the patient always extinguished the left stimulus on double target trials. Similarly, when the cross with the two box display appeared in the left hemispace, all of the stimuli left of the cross were extinguished on double target trials. However, when the cross with the boxes appeared in the right hemispace still 70% of the stimuli left of the cross went unreported after double target presentation.

Humphreys et al. (1994) reported two cases of visual extinction in the vertical dimension. Two stimuli were presented simultaneously above and below a central fixation point. Detection of two stimuli was impaired compared with the detection of one stimulus. The patients' response pattern did not follow a spatial bias.
In a different experiment, Di Pellegrino and De Renzi (1995) altered the stimulus properties of the leftmost stimulus. The data showed that even when the size of the normally extinguished stimulus was increased fourfold, a significant improvement in the performance was not achieved.
However, Ward et al. (1994) reported that grouping of the stimuli can reduce visual extinction. In a simple detection task, two visual extinction patients were required to report whether one or two or no stimuli were presented in the left and right visual field. The number of extinction errors for the stimulus projected into the left visual

field was reduced drastically when the left-sided stimulus formed a good perceptual group with the stimulus in the right visual field with respect to symmetry, similarity or familiar configuration. A processing advantage for intact compared to scrambled objects was documented by Ward and Goodrich (1996) in two right hemisphere damaged patients. On bilateral presentation, the performance of the extinction patient improved dramatically when the object in the left visual field was "good". Scrambled objects in the left visual field were significantly more often extinguished.

Humphreys et al. (1994) discovered an interaction between different stimulus types. When a word and a picture were presented simultaneously below and above a fixation point, words were consistently extinguished. Even when words appeared at the location of the fixation point, the focus of attention, and pictures were projected above and below the fixation points, pictures were favoured by visual selection. A different issue is the level of processing of the extinguished stimulus.

Di Pellegrino and De Renzi (1995) tested the interference between extinguished and perceived stimulus in a simple reaction time task. Strings of X and O were projected into each hemifield. The instructions given to the patient were to respond only to the presence of a sequence of X's. In the condition where a sequence of O's was shown in the impaired hemifield and a string of X's in the intact hemifield the reaction times increased significantly indicating that the stimulus of which the patient was not aware influenced his behaviour.

In a seminal study, Volpe et al. (1979) reported that in a same/different task patients were able to make use of the information in the impaired field. In the bilateral condition, the four patients reached levels of accuracy between 88% and 100% whereas the patients performed significantly worse in the naming task of the extinguished stimulus. Two of the four patients did not report any stimuli at all from the impaired visual field in the naming task. The third subject named 48% of the objects correctly and the fourth patient 23%. These figures, however, were significantly lower than in the same/different condition. Volpe et al. (1979) interpreted their results as evidence for a disruption of information flow to conscious awareness. Farah et al. (1991) questioned this conclusion and argued instead that dissociation of the performance between the same/different task and the naming task might have been caused by different processing requirements. It was argued that

much less visual information is required to perform accurately in the same/different condition than to name an arbitrary object correctly. For this reason, Farah et al. (1991) substituted the naming task with a forced choice task ("did you see a ... or a ...?" - the names of the two objects would be given). The dissociation disappeared consequently. This result was considered evidence for a perceptual impairment.

Some support for Volpe et al. (1979) was provided by Berti and colleagues (1992). Their study followed closely Volpe et al.'s method (1979) with one exception. Bilateral presentation of the same object included three conditions: The two objects in each hemifield were completely identical, the same object which appeared in the impaired hemifield was shown under a different perspective and, finally, the object in the impaired hemifield was different but from the same category than the object in the intact hemifield. In all conditions, the patients performed above chance whereas the naming of the objects was significantly impaired. Although Farah et al.'s position (1991) still holds that a same/different judgement is more easily achieved than naming the object, the study by Berti et al. (1992) demonstrated that their patients based their decisions on some high level processing of categorical information.

In the next section, various theories will be presented that attempt to account for the extinction phenomenon.

6.4. Theories of extinction

6.4.1. A sensory approach

De Renzi et al. (1984) expressed support for Bender's account (1952) that extinction is basically a sensory impairment and is to be separated from neglect. This conclusion was based on three considerations. Firstly, no significant lateralisation was found for extinction whereas unilateral neglect appears to be associated more frequently with right hemisphere lesions. Secondly, extinction can be doubly dissociated across modalities. After analysis of the CT-scan data, De Renzi et al. (1984) suggested that the different lesion sites seemed to be related to the disruption of discrete anatomical substrates, specific for each modality. Finally, three of the right hemisphere patients displayed clear signs of neglect but had no difficulties in the perception of two simultaneous stimuli (see also De Renzi et al., 1989b).

An anatomical study by Vallar et al. (1994) also suggested that extinction might have a sensory component. A comparatively high frequency of subcortical lesions including the ascending pathways was considered as a possible neural correlate of this sensory component of extinction.

Eidelberg and Schwartz (1971) conducted anatomical studies with monkeys who received lesions to different parts of the central nervous system under controlled conditions. Eidelberg and Schwartz (1971) concluded that tactile extinction is the consequence of a reduced somato-sensory input "via one spinothalamic tract or by reduced functional mass in areas concerned with somatic sensation in one hemisphere relative to the other" (Eidelberg & Schwartz, 1971, p.106).

6.4.2. A perceptual approach

Denny-Brown et al. (1952) linked extinction to the disruption of normal functioning in the parietal cortex. According to this view, the parietal cortex is associated with the "first stages of perception, spatial summation of sensory information and ... the recognition of form" (Denny-Brown, 1952, p.469). The term 'morphosynthesis' was introduced by the authors to describe this integrative function of the parietal lobe. Accordingly, when the parietal cortex is damaged, impaired spatial summation leads to the perception of degraded information from the contralateral side ('amorphosynthesis'). On unilateral stimulation, this deficit might not become obvious but as soon as there are rivalrous stimuli from the ipsilesional side, the "combination of stimuli is treated as a unitary whole, within which poorly differentiated features are eliminated" (Denny-Brown, 1952, p.469). However, the amorphosynthesis theory fails to account for extinction caused by lesion sites other than the parietal area (see Vallar et al., 1994).

6.4.3. A representational account

A rather general account was presented by Bisiach (1991) who attributed extinction to a deficit in the processes of neuronal mapping of spatial relationships. According to Bisiach (1991), the dysfunction can arise at many different levels of spatial representation which might be one of the reasons for the confusing heterogenity of the phenomenon extinction. Bisiach (1991), though, failed to apply his view to

specific aspects of extinction. Support for a representational account of extinction came from Bellas et al. (1988) who examined right hemisphere extinction patients in the olfactory modality. The patients failed to respond to their left contralesional nostril on olfactory double simultaneous stimulation. The olfactory system is different from other modalities in that it is ipsilaterally innervated. Therefore, the extinguished left sided stimulus was extinguished in the left hemisphere. Bellas et al. (1988) interpreted these findings as concordant with the predictions of the representational theory.

6.4.4. Attentional theories

Denny-Brown et al. (1952) observed altered attentional behaviour of their patient, but the changes in the ability to allocate attention were regarded as an epiphenomon by the authors. "The fundamental defect was deeper, and independent of this 'inattention' " (Denny-Brown et al., 1952, p.468). Bender (1952), too, maintained that impaired attentional processes are not a tenable account for extinction since attempts to draw attention to the impaired hemifield do not improve perception - a claim that was refuted by several studies (e.g. Di Pellegrino and De Renzi, 1995; Furmanski, 1950; Kaplan et al., 1990 and see also Mattingley et al., 1998).

On the other hand, Critchley (1949) associated extinction strongly with impaired attentional processes. For Critichley (1949), tactile extinction is equivalent to tactile inattention. The damaged brain cannot attend to two simultaneous stimuli. The stimulus from the impaired hemifield "which is of lesser intensity, or which proceeds from a segment of higher limen, or from regions which have become less obtrusive within the bodyscheme" (Critchley, 1949, p.555) is extinguished in favour of the ipsilesional stimulus.

The role of impaired attention processes was also stressed by Heilman (1979). According to the limited attention or capacity theory, each hemisphere has an attentional bias mainly towards the contralateral space. In addition to normal contralateral orienting, the right hemisphere can also attend efficiently to ipsilateral stimuli (Heilman, 1987). Normally, bilateral stimuli are processed simultaneously. If, however, one hemisphere ("usually the right"; Heilman, 1993, p.301) is traumatised, its orienting capacity might be impaired. The intact ("left"; Heilman, 1993, p.301)

hemisphere might determine recovery from unilateral inattention but the intact hemisphere might not only have an attentional bias towards the contralateral hemispace but also a limited capacity to allocate attention. For this reason, on bilateral simultaneous stimulation the intact hemisphere will be limited in the perception of ipsilateral stimuli.

An extension of this theory was put forward by Rapcsak et al. (1987). It was proposed that damage to the corticolimbic-reticular system impairs attentional capacity. Extinction was defined as a measure of unequal distribution of attention along a gradient in the entire binocular visual field with a maximum of attentional resources for the most ipsilesional stimulus and a minimum for the most contralesional stimulus. This interpretation has similarities to Kinsbourne's orientational bias model who postulated attentional gradients across the two hemifields (Kinsbourne, 1987). To account for the attentional gradient, Rapcsak et al. (1987) referred to anatomical studies. In these studies (Rizzolati et al., 1981, 1985), it was claimed that, whereas the area of the visual field around the midline falls into the receptive fields of attention-related neurons of both hemispheres, the eccentric space of each hemispace is subserved exclusively by the contralateral hemisphere. As Di Pellegrino & De Renzi (1995) pointed out Rapcsak et al.'s (1987) concept of an attentional gradient is static as the attention-related neurons possess invariant activity. Consequently, any stimulus (even unilateral) should be extinguished in the periphery of a contralesional field after cerebral damage. This is not the case in extinction. On the other side, Kinsbourne's orientational bias model (Kinsbourne, 1987) is dynamic in assuming opposing hemispheric processors which control deployment of attention and are mutually inhibitory. Orienting of attention is determined by a vector. This vector is a product of the interaction between the two processor which both have a bias to the contralateral side. To account for the higher incidence of neglect, it was postulated that the orientational bias is much stronger in the left hemisphere. Unilateral damage would result in a directional imbalance across both hemifields towards the contralateral side of the intact processor. Whereas Rapcsak et al.'s (1987) claim of a limited capacity system in the intact hemisphere appears as to be an ad hoc solution, Kinsbourne's orientational bias theory (1987) provides a much more coherent account of the extinction of the contralesional

stimulus on unilateral presentation both in the contralesional and ipsilesional hemispace with respect to the damaged cerebral hemisphere (Di Pellegrino & De Renzi, 1995; see also Làdavas, 1990). However, both theories cannot explain the lack of hemispheric lateralisation of unimodal extinction (Weinstein, 1994).

A different reading of extinction was put forward by Ward et al. (1994). It was suggested that extinction might be a spatially specific exaggeration of a normal attention limitation where a contralesional stimulus loses out in the competition for selection. A well-established attentional phenomenon is the difficulties normal subjects experience in judging simultaneous visual targets (Duncan, 1980). This normal attentional limitation only occurs when the two sets of target attributes (each belonging to the two simultaneously presented stimuli) are part of two separate objects (Baylis et al., 1992; Duncan, 1984).

Ward et al.'s prediction (1994) that grouping of stimuli might ameliorate extinction was borne out by the results. Other studies reported extinction-like phenomena in normals. Benton et al. (1972) reported "obscuration" in a group of normal subjects. Obscuration is defined as a milder form of extinction. In obscuration a stimulus is perceived as weaker on double simultaneous presentation compared to when applied without a second stimulus. Benton et al. (1972) tested five normal subjects in a magnitude estimation task. The subjects were required to estimate test weights applied to the forearm. Three subjects were tested on the right and two on the left arm. On bilateral stimulation, a much heavier masking stimulus was dropped on the other arm. The results demonstrated that the mean magnitude estimate for every test weight decreased from the single to the double stimulation condition. These findings led Benton et al. (1972) to suggest that "the clinical phenomena of extinction and obscuration are exaggerated expressions of a normal physiologic mechanism" (Benton et al., 1972, p.1181). In a series of tachistoscopic search experiments, Pollmann (1996) detected a pop-out induced extinction-like phenomenon in neurologically intact subjects. Highly salient (pop out) distractor stimuli increased reaction times to less salient contralateral target stimuli. However, this effect emerged only with a right visual field distractor and a target stimulus in the left visual field. In the reverse condition, the distractor stimulus had no influence on the

reaction time to the target. These findings provided further support for Kinsbourne's (1987) orientational bias theory.

6.4.5. Theories based on interhemispheric interaction and another two attentional theories

A different line of argument was presented by Nathan (1946) who postulated suppression of the damaged cortical areas by intact ones through interhemispheric interaction. It is further claimed that this interhemispheric suppression occurs only after occipital and occipito-parietal lesion.

Along similar lines, Furmanski (1950) proposed a high perception threshold due to increased interaction of ipsilesional and contralesional suppressor areas and thalamic relay centres.

Birch et al. (1967) presented the 'inertia-interference' model which has many similarities to the theory presented in this thesis. Birch et al.'s (1967) model is based on the following three assumptions: First, cerebral damage causes "increased inertia reflected in slower processing of information" (Birch et al., 1967, p.128). Second, the cerebral damage leads also to an increased refractory period in the affected hemisphere. Third, the damaged hemisphere is inhibited by the intact half. Birch et al. (1967) examined 19 left hemiplegic extinction patients. Low intensity electric shocks were administered to the left and right fore arms. The stimuli were presented in different conditions: Simultaneous presentation, the left sided stimulus preceded the right one by 300 or 600 ms, and finally the right fore arm was stimulated 300 ms or 600 ms before the left arm. The patient was asked to report the presence of any stimulus. In the condition where the stimulus to the left arm preceded the one to the right, 16 patients improved significantly compared to simultaneous stimulation when the interstimulus interval was 300 ms and 15 patients were aware of two stimuli with an interstimulus interval of 600 ms. Analysing the individual responses it was shown that all 19 patients improved in either the 300 ms or 600 ms condition. In 14 patients extinction was reported to be eliminated completely and in the remaining five patients extinction behaviour was reduced. Furthermore, a shift of lateralisation of extinction was reported with increase of the interstimulus interval. On simultaneous bilateral presentation, 80% of the stimuli were extinguished on the contralesional

side and 8% on the ipsilesional side. When the left arm was stimulated before the right arm at an interstimulus interval of 300 ms, 74% of the stimuli went unreported on the contralesional side compared to 21% ipsilesionally. This relationship changed further on increasing the interval to 600 ms in the same condition where only 50% of stimuli were extinguished contrallesionally and 46% of stimuli were now not reported on the intact side. Stimulating the right side before the left, however, yielded a similar performance pattern as in the simultaneous condition.

Birch et al. (1967) argued that maybe "inhibition in the intact nervous system is the product of differential timing of activation and of the selective interference of the organization of one input by the other" (Birch et al., 1967, p.124). Based on this theory, it was predicted by the authors that extinction might be ameliorated by increasing the relative intensity of the extinguished stimulus. Denny-Brown et al. (1952) reported that by gradually increasing the multiplicity of a stimulus on the affected side extinction would eventually disappear and both stimuli were perceived. On the other hand, Di Pellegrino and De Renzi (1995) did not achieve an improvement in the extinction performance of their patients by lengthening the presentation time of the extinguished stimulus or by augmenting its size four-fold compared to the stimulus in the intact field.

Also, in particular the theories of Nathan (1946) and Furmanski (1950) that are based on interhemispheric inhibition are not supported by Eidelberg and Schwartz's study (1971). In the latter study, it was reported that despite a severed corpus callosum subsequent cortical lesions caused extinction "thus ruling out interhemispheric inhibitory influences via this system" (Eidelberg & Schwartz, 1971, p.106). Birch et al.'s account (1967) only partly falls into this theoretical category because an additional mechanism, the slowing down of neuronal processing, is claimed independent of inhibitory interhemispheric mechanisms.

A paradigm similar to the one applied by Birch et al. (1967) was used by Rorden et al. (1997) who examined two patients with left sided extinction. The patients were asked to fixate on a central cross that was presented on a computer screen and to report on which side the stimulus had appeared first. Then, two horizontal bars were presented to each visual field. The bars could appear simultaneously on the screen, or they were presented offset to each other by an interstimulus interval ranging from 14

to 864 ms with the left bar appearing before the right in one condition and vice versa in the other condition. It was found that the left sided stimulus required a temporal lead of 200 ms to be perceived before the stimulus in the right visual field. Rorden et al. (1997) interpreted their results as a prior-entry phenomenon or in other words as evidence for an ipsilesional attentional bias in extinction. The prior entry law postulates that an attended stimulus will be perceived before a physically simultaneous stimulus that is unattended.

Rorden et al.'s (1997) findings did not support Posner et al.'s (1984) account of extinction. The act of covert attention is accomplished with three different mental operations: Disengagement of attention form the current focus, shifting attention to the new target and engagement of attention with the new target. According to Posner et al. (1984), the disengagement operation is affected in extinction patients who have suffered parietal damage and is not observed in patients with trauma to frontal, temporal and midbrain structures of the brain. However, Rorden et al. (1997) argued that the extinction patients in their study (both had suffered damage to the temporo-parietal area) displayed abnormal perception even if the contralesional stimulus had appeared first on the contralesional side of the screen, even with temporal leads up to 200 ms. Under these circumstances, there was no ipsilesional stimulus the patients had to disengage attention from first.

7. Summary and conclusion

At the end of this review chapter, we have to conclude that neglect appears to be a highly heterogeneous syndrome (Cubelli et al., 1991; Stone et al., 1998). The number of lesion sites that have been associated with unilateral neglect and the diverse cluster of neglect-related symptoms that can all dissociate from each other suggest that unilateral neglect is "not an empirically well-founded or theoretically-coherent entity" (Halligan & Marshall, 1992, p.525). This view implies that there will be no single theory of neglect which will succeed in accounting for the disorder with all its facets.

Indeed none of the neglect theories discussed above have offered a convincing account of neglect in its entirety. Nevertheless, it appears that the majority of researchers favour an analysis of neglect where, in one form or the other, the

underlying impairment is interpreted as malfunction of normal attentional processes (Heilman & Valenstein, 1972; Watson et al., 1973; Heilman et al., 1993; Kinsbourne, 1970, 1970b, 1977, 1987, 1993; Mesulam, 1981; Posner et al., 1984; Posner & Raichle, 1994; Rizzolatti & Camarda, 1987; Riddoch & Humphreys, 1987; Robertson, 1989; Làdavas et al., 1990; Cubelli et al., 1991; Chatterjee et al., 1992; Halligan & Marshall, 1994; Marshall & Halligan, 1994).

Before we proceed to the discussion of our own theory, we will first present a historical review of the concept of attention and will introduce some neuroanatomical and -physiological data on this topic. The latter will be particularly relevant as our theory is tightly constrained by neuropathological evidence.

Chapter Three

Selective Attention - A review

This chapter will present a general overview of the main theories of selective attention in humans. Special emphasis will be put on visuo-spatial attention. In the second half of this chapter, neuroanatomical and -physiological aspects of selective attention will be addressed.

1. Introduction

William James (1890) succinctly said of attention that "everyone knows what it is". He continued, it "implies withdrawal from some things in order to deal effectively with others" (quoted by Walsh & O'Mara, 1994).

More recent definitions have employed terms like mental effort, selection, search or concentration (Johnston & Dark, 1986). Selective attention is perceived as a controlled process which is associated with consciousness (Posner & Rothbart, 1998). The concept of attention as mental effort is based on the general assumption that central processing is a limited capacity system (Broadbent, 1958, 1982; Shiffrin & Scheider, 1977; Duncan, 1980). This common view has been questioned, though, by a minority of researchers who have either discarded the idea of limited capacity altogether (Neisser, 1976) or postulated multiple sets of limited capacity systems (Wickens, 1984). However, agreement seems to exist about the selective nature of processing.

Johnston and Dark (1984) have proposed the following simple definition: "Selective attention refers to the differential processing of simultaneous sources of information" (Johnston & Dark, 1986, p. 44). The source of information can either be internal (memory and knowledge) or external in nature (objects and events from the environment). As for the latter, one has to distinguish further between bottom-up (data-driven) and top-down (internally driven) processes. In bottom-up processing, representations of a stimulus are generated on various levels which can range from

sensory to complicated semantic analyses. Available processing levels that have been created by previous experience (for example learning), and the structure of the stimulus with its physical (clarity, intensity) and content properties determine to what level processing is completed. Conversely, in top-down computation, processes are biased internally towards specific stimuli. In the relevant literature, the majority of studies have been concerned with the top-down control of selective processing (Johnston & Dark, 1986).

Cherry (1953) has encapsulated the principal characteristics of selective attention in the formulation of the "cocktail-party problem". On the one hand, people do not find it difficult to focus on and follow a conversation in the midst of the noisy environment of a cocktail-party. On the other hand, they are still capable of picking up potentially relevant information, like one's name, in other conversations. The former situation illustrates the focused-attention aspect of selective attention whereas the latter is an example of the divided-attention aspect of attention. The question is how can one focus and divide selective attention at the same time? In the following section, the major groups of attention theories will be reviewed.

2. Theories of selective attention

Attention theories are commonly divided into two major classes: Those theories that regard attention as a causal mechanism of selective processing and the group of theories that consider selective processing the product of other processes. James (1890) coined the terminology which is still in use and called the former category 'cause theories' and the latter 'effect theories' (Johnston and Dark, 1984).

2.1. Cause Theories

The majority of recent theories of selective attention has postulated two qualitatively different domains of stimulus processing (e.g. Broadbent, 1958, 1982; Posner & Boies, 1971; Kahneman, 1973; Shaw & Shaw, 1977; Shiffrin & Schneider, 1977; Duncan, 1980; Julesz, 1984; Lavie, 1995): The first, let us call it domain A, has been assigned attributes like non-conscious, automatic, peripheral, intraperceptual, pre-attentive, passive and possessing a large processing capacity. Domain B, on the other

hand, has been called conscious, controlled, central, extra-perceptual, attentive and active with a limited processing capacity.

The 'bottleneck' in information processing has led to the requirement of selection. In other words, domain B acts as a attentional mechanism or "cause of selective processing" that directs its limited capacity to the selection of perceptual representations created in domain A for "entry or translation into consciousness" (Johnston & Dark, 1986, p.66).

There is general agreement about the importance of selective mechanisms. However, the opinions differ with regard to the locus of selection in the sequence from perception to action. The early selection approach (Broadbent, 1958, 1982; Kahneman, 1973; Treisman & Gelade, 1980) assumed that perception is a limited process that requires selective attention to proceed. For this reason, attentional selection happens early after basic analysis of physical features in order to distinguish between selected and unselected items. Consequently, only selected stimuli complete processing in domain A and are subsequently perceived fully. By contrast, the late selection theory claims that perception is an unlimited process which proceeds in an automatic parallel way that does not require any selection (Deutsch & Deutsch, 1963; Posner & Boies, 1971; Shiffrin & Schneider, 1977; Duncan, 1980). Accordingly, selection occurs only after full perception to provide the relevant response. In other words, the selection process of domain B has no influence on the processing fate of unselected stimuli in domain A. It is the latter approach, the late selection account, that has received more support in recent years (Lavie, 1995).

We will now present one representative theory from each theoretical group in more detail to highlight the differences of opinion.

2.1.1. Early selection

Broadbent (1958, 1971, 1982) proposed mechanisms that control information flow between domain A, an unselective sensory information store, and domain B, the limited capacity system. According to this model, biased selection takes place from domain A "before the complex of features ... has been identified as an instance of

some category" and information will only be processed completely, if it has been selected (Broadbent, 1982, p.260). The biasing mechanisms put forward by Broadbent are *filtering*, *categorising* and *pigeon-holing* (Broadbent, 1971, 1982). "Filtering ... is the selection of certain items for analysis and response, on the basis of some common characteristic possessed by the desired stimulus", for example some physical features (Broadbent, 1971, p. 177). The second selection mechanism is categorising. This term refers to a selection process which is based on aspects of a stimulus that make it a member of a particular class or category. Once categories have been created, a third selection process can become operational, pigeon-holing. Pigeon-holing operates by introducing a processing bias to certain sets of information.

Different predictions emerge depending on when selection occurs: According to the early selection theory, unselected items should not have any effect on selected stimuli, whereas the late selection account postulates interference.

In Broadbent's first version of his theory (1958), a filter was postulated that blocks out all unselected information created in domain A. Later, based on a series of papers published by Treisman (1960, 1964, 1969), the filter function was re-defined as being "attenuating" (Treisman, 1960, p.246) rather than blocking with regard to non-attended sources of information. Treisman (1960) published the following data that were incompatible with a Broadbent's original filter theory (1958): Two messages were presented dichotically and the subjects were required to repeat what they heard in one ear. Approximately in the middle, the two passages were switched to the opposite ear. The results showed that subjects occasionally reported one or two words at the break from the unselected ear. This behaviour was incompatible with Broadbent's definition of a filter that operated as an all-or-none barrier (1958).

Within the context of the cocktail-party phenomenon, the filtering mechanism based on sensory features would explain the focused-attention aspect, whereas pigeon-holing would accommodate the divided-attention problem. "Pigeon-holing ... is like filtering in that it selects some events for further processing. Instead of selecting the events by a unique feature, however, this strategy operates by applying a bias to

certain categories, so that they will be triggered off by less evidence than they would normally need" (Broadbent, 1982, p.260). So, one would hear the mention of one's name in the neighbouring conversation because all information under the category "matters concerning oneself" has been allocated a processing bias through the mechanism of pigeon-holing.

2.1.2. Late selection

To illustrate the late selection account we will outline the proposals of Shiffrin and Schneider (1977). The theory was embedded in their work on controlled and automatic information processing. Shiffrin and Schneider (1977) postulated a domain A where representations were encoded fully without interference from a "tightly capacity-limited" domain B (Shiffrin & Schneider, 1977, p.156).
Two kinds of selective attention emerge in this framework: "Automatic attention response" and controlled search. An automatic attention response can be elicited by a pertinent feature which has been generated in domain A. The automatic response will then focus controlled processing via an attention director to the relevant feature. However, if there is a variety of non-relevant features the "various attention responses will conflict and cancel each other" (Shiffrin & Schneider, 1977, p.164). In this case, the subject is forced to resort to a controlled search strategy to detect relevant features in the output of domain A.
In other words, to refer back to the cocktail-party problem, controlled attention processes can account for the focused-attention phenomenon, whereas automatic attention responses ensure that potentially relevant information outside focused attention is not lost.

The early and late selection discussion has not reached any consensus. However, Lavie (1995) proposed a compromise between the two positions. "The late and early selection debate may be resolved if perceptual load of relevant information determines the selective processing of irrelevant information" (Lavie, 1995, p.451). More specifically, if the processing load of the task exhausts all available capacity, irrelevant items will not be perceived. However, if the processing demands of the relevant stimuli are low, any spare capacity is automatically allocated to the

irrelevant items. Lavie's theory (1995) has recently received support from Rees and Frith (1998) who provided evidence from behavioural and functional magnetic resonance studies. It was shown that under conditions of low processing load, the neurophysiological signal of the irrelevant stimulus was associated with increased activation and vice versa.

Johnston and Dark (1986) have emphasised a serious metatheoretical problem inherent in all cause theories. These theories are quite successful in accounting for a number of empirical data related to selective attention. However, they are all based on the assumption of some mental agent which controls selection of stimulus information. "Domain B has all the characteristics of a processing homunculus" (Johnston & Dark, 1986, p.68). The next logical question would be to ask how the processing homunculus pays attention. At this point, cause theories cannot give an answer. We will now turn to effect theories.

2.2. Effect Theories

James (1890) was one of the earliest advocates of effect theory. In more recent years, Neisser (1967, 1976), Hochberg (1978) and Desimone with his colleagues (Desimone et al., 1990; Desimone & Duncan, 1995; Desimone, 1998) have advanced similar theories.

According to James, "attention creates no idea; an idea must already be there before we can attend to it". He continued: "We see how we can attend to a companion's voice in the midst of noises which pass unnoticed though objectively much louder than the words we hear. Each word is *doubly* awakened; once from without by the lips of the talker, but already before that from within by the premonitory processes irradiating from the previous words, and by the dim arousal of all processes that are connected with the 'topic' of the talk" (James 1890, p.450; quoted by Johnston & Dark, 1986).

Within his theory of analysis-by-synthesis Neisser (1967, p.103) defined the direction of attention towards an object as the "attempt of a more extensive synthesis" of the object beyond the preliminary processing stages of a parallel pre-attentive system. Attention itself referred to constructive processes involved in

the synthesis of the inner representation of an object. Subsequently this representation is matched with the sensory input. Referring to Treisman (1960) and Broadbent (1958), Neisser (1967, p.213) wrote: "Irrelevant, unattended streams of speech are neither 'filtered out' nor 'attenuated'; they fail to enjoy the benefits of analysis-by-synthesis".

A very similar view was proposed by Hochberg (1978) according to which attention was defined as a plan-matching and schema-testing mechanism. Plans or schemata are units of information through which an individual can encode more information than he/she can retain from individual items.

The 'biased competition' model by Desimone and his colleagues (Desimone et al., 1990; Desimone & Duncan, 1995; Desimone, 1998) represents a neurophysiological account within the effect theories. For this reason, their theory will be presented in the section that examines neuronal mechanisms of attention.

To summarise, all these theories share the assumption that selective encoding is a constructive rather than analytic process and that it is based on natural priming processes. Both aspects of the cocktail-party effect are accounted for by chronically active schemata. The great advantage of effect theories is that they avoid the homunculus problem which has been addressed above (Johnston & Dark, 1986).

In the next section, we will address the spatial aspect of selective attention or in other words the selective allocation of attentional process to particular spatial co-ordinates.

3. Visuo-spatial attention

3.1. The attentional focus

One of the most popular analogies about how attention is allocated in space compares the focus of attention with the beam of a 'spotlight'. This attentional beam can be characterised in the following way: First, it moves from one point in space to the other, second, the movement is analogue instead of jumping from one co-ordinate to the other, and third, the diameter of the beam possesses a specific size.

A frequently used technique to measure the efficiency of information processing at different locations in space is the cost-benefit paradigm which had been proposed by Posner and his colleagues (1978, 1980). In this set-up, differences in reaction times

to a stimulus at expected and unexpected positions in the visual field are measured with the eyes remaining on a central fixation point. The subject is shown either a plus sign or an arrow pointing to the left or right side. If the plus sign appears on the screen the stimulus is just as likely to occur in the left as in the right visual field. If an arrow is shown, the stimulus can appear either on the indicated side (valid trial) or on the opposite side (invalid trial). All visual cues are shown in a central location. In this paradigm, both a benefit of knowing where the stimulus appears and a cost of not knowing where the stimulus is shown can be established. The following response pattern emerged: Reaction times in trials where no informative clue is given are faster than the ones in invalid trials and slower than the ones in valid trials. The results from this paradigm have therefore suggested that in the condition where an informative cue is given, attention occurs in a focused or serial processing mode. In the non-cued condition, attention seems to be distributed evenly over the entire display with parallel processing of the display stimuli.

Based on these findings a number of attentional models of selection were proposed (Hoffman, 1978, 1979; Duncan, 1980; Jonides, 1983). Eriksen and his colleagues (1985, 1986) presented a model that used a 'zoom lens' analogy. According to this view, the diameter of the attentional beam was variable instead of being restricted to either one relatively small or one wide diameter. In connection with the zoom-lens model, Eriksen and St. James (1986, p.225) asked three questions: "1. Can the spatial extent of the attentional focus be made to vary in response to precues? 2. As the area of the attentional focus increases, is there a decrease in processing efficiency for stimuli within the focus? 3. Is the boundary of the focus sharply demarcated from the residual field, or does it show a gradual drop-off in processing resources?"
In a review paper, Umiltà (1988) proposed the following preliminary answers to the above questions: The data with respect to the first question were affirmative. It appears that the size of the attentional focus does vary and change depending on task demands (Beck & Ambler, 1973; LaBerge, 1983; Shulman et al., 1985; Eriksen & St. James, 1986). The question whether the diameter of focus is inversely related to processing efficiency has generated much more controversy in the field. Some studies supported the predictions made by the zoom-lens model (Egeth, 1977;

Eriksen & St. James, 1986) others did not (LaBerge, 1983). As for the final question, not many studies have investigated this problem. However, evidence has suggested a processing gradient on the borders of the attentional focus (Eriksen & St. James, 1986).

In the next section, we will deal with the problem of how the attentional focus is directed across a visual array.

3.2. Orienting of the attentional focus

Mainly through Posner's work and the development of the cost-benefit paradigm (1980; Posner et al., 1978) clear support was finally provided for the long-held intuition that attention can be allocated both overtly and covertly. Overt shifts of attention are accompanied with head and eye movements whereas covert attention allocation can be performed without any body movements. The differences in reaction times between the valid versus neutral trials and the neutral versus invalid trials represent the benefits and costs which can be attributed exclusively to the covert orienting of attention. Needless to say, the trials are taken into account only when the test subjects have not moved their eyes from a central fixation point.

Apart from the horizontal and vertical dimensions, orienting of covert attention can also be achieved in the sagittal plane (Gawryszewski et al., 1987) but, as He and Nakayama pointed (1995) out, the focus of attention cannot be directed efficiently to arbitrary depths and extents in space. The allocation of attention is rather linked to perceived surfaces. Interestingly, there are differences in the speed to detect unexpected stimuli in the different dimensions. In the sagittal plane, far stimuli take longer to be responded to compared to near ones (Gawryszewski et al., 1987). Unexpected left-sided stimuli are detected more slowly than right-sided ones in the horizontal plane whereas there seems to be no difference along the vertical dimension (Gawryszewski et al., 1987; Rizzolatti et al., 1987).

Another dichotomy within the context of attentional orienting differentiates between voluntary and automatic shifts of the attentional focus although this distinction has become controversial (Theeuwes, 1994). Advocates of the dichotomy have claimed

that some stimuli have reflexive control over attention allocation and in other cases a subject can voluntarily shift the focus of attention from one area to another.

For example, Jonides (1981) proposed that peripheral cues automatically attract attention whereas allocation of attention to central cues is under voluntary control of the subject. To test these predictions, Jonides (1981) modified the cost-benefit paradigm by using both peripheral and central cues (Posner, 1980, and Posner et al., 1978, had only used central cues). Three empirical criteria were chosen to define automaticity: Minimal use of mental capacity, resistance to suppression and the influence of expectation. To test the first criterion, subjects were asked to perform a memory span task during the visual search. It was predicted that the attention capturing power of the peripheral cues was relatively unaffected by the processing demands of the memory task which was confirmed by the data. In a second experiment, it was tested whether the response patterns to peripheral cues showed resistance to suppression and whether the central cues could be ignored by the subjects. Although there was evidence that subjects had some control over the decision whether to attend to a peripheral stimulus or not, the data confirmed a difference in the processing of central and peripheral cues. As for the last criterion, Jonides (1981) demonstrated that, in accordance with his prediction, the assumed automaticity of the peripheral cues rendered it less subject to the influence of expectancy. A further interesting finding of this study was that peripheral cues were more effective in drawing attention because, compared to central cues, they produced greater cost-benefit effects.

A further difference between central and peripheral cues was found in connection with the so-called inhibition effect. This phenomenon describes the slowing down of the response to a peripheral stimulus which appears in exactly the same location as its preceding cue that has attracted the covert attention of the subject. No inhibition effect has been established when covert attention was allocated to a central cue (Umiltà, 1988).

After having described some characteristics of attentional orienting, we will now turn to the problem of how attention moves from one location to another.

3.3. Mechanisms of attention shifts

Shulman et al. (1979) were one of the first teams who tried to describe the characteristics of attentional movement. The motivation was to illuminate the basic question whether the movement of attention can be described in terms of an analogue or discrete operation. Consider the shift of attention from location A to location C. B is labelled as the point in space between A and C. Attentional movement is classified as analogue if a shift from A to C includes attending to B. Discrete movement on the other hand describes a shift from A straight to C without attending to B. Shulman et al. (1979) used a reaction time task very similar to the cost-benefit paradigm. "The analogue-discrete issue can be explored by looking at reaction time to events at points B and C as a function of the time following the instruction to move attention from A to C" (Shulman et al., 1979, p.523). Therefore the following predictions were made: If movement is analogue, reaction times to a target at location B are fast relative to a target C at an early stage during the shift of attention. At a later stage of the attentional movement, reaction times to target at location C are speeded up relative to target B because attention is moving closer to C. Conversely, if the discrete movement theory holds true, no improvement at location B relative to C should ever be observed. It is only reaction times to the target in location C which improve during the course of attention shift. After analysis of the data, Shulman and his colleagues (1979) supported the analogue model. Similar results were produced by Tsal (1983) who also favoured the analogue nature of attentional shift.

However, Remington and Pierce (1984) advocated a discrete mode of movement. The motivation in this study was to analyse the effects of distance on the time to shift attention. The data provided evidence that the time it takes to move attention from A to C is invariant and independent from the distance between the two points. This result was interpreted as support for a discrete model of attentional shift. In their study, Remington and Pierce (1984) have broached another interesting question of attentional shift. It addressed the issue whether attention travels at constant velocity or at a constant time. If attention travels at a constant speed, the cost, or in other words the increased reaction times to an unexpected stimulus, is a function of the distance between the cued location and the location of the unexpected target. This

prediction was supported by the studies of Shulman et al. (1979) and Tsal (1983) whereas Remington and Pierce (1984) provided support for the latter scenario.

However, movement of attention is not a necessary mechanism to account for cost effects at unexpected target locations. Hughes and Zimba (1985) have proposed a model similar to the framework of Broadbent's (1958, 1971) filter theory. According to the filter theory, information within the attended location is processed whereas information outside the attended location is filtered or attenuated. Hughes and Zimba (1985, p.425) reported that according to their results "visual attention was not a spatially restricted phenomenon; rather, it extends throughout the visual hemifield". No cost or benefit effects were found at all when the cued location and the point of the unexpected target were in the same hemifield (but see Rizzolatti, 1987, who found effects within the hemifield). Effects only emerged across the vertical meridian, i.e. across the two visual half fields. Furthermore, it was reported that preliminary results point towards a similar processing division along the vertical axis. Hughes and Zimba (1985) subsequently proposed that attention is spread evenly across the cued hemifield. Cost and benefit effects in the non-attended hemifield are due to "inhibition throughout the opposite hemifield" (Hughes & Zimba, 1985, p.428). This stance clearly rejected the analogy of the attentional spot-light.

Yet another approach which was not based on the idea that attention is moved across a visual array can be found in a study by Shulman et al. (1985). The idea was put forward that a gradient of attention extends outward from the centre of attention. In other words, attentional capacity is spread over a large area, if not over the entire visual field (Umiltà, 1988). However, processing capacity is distributed in a particular fashion with the maximum of capacity at the centre of the attentional focus and a gradual decrease of capacity towards the periphery.
Shulman et al. (1985) performed a simple reaction time experiment. Subjects were required to shift their attention covertly to a cued spatial location and react to a subsequently presented target light. The target appeared at the cued location on 77% of the trials. On the other trials it was presented at different eccentricities. By analysing the reaction time to the target as a function of the distance of the target

from the cue and the eccentricity of the cue, the distribution of attention at different eccentricities was calculated. The results suggested that attention is spread over a larger area in the periphery compared to foveal areas. Consequently, information at the centre of a peripheral focus will be processed less efficiently.

Before proceeding to present neuronal mechanisms of attention, we would like to point out an issue concerning spatial attention that has not been mentioned up to this point. In the above pages the concept of attention was dealt with in a purely spatial framework which suggests that attention is directed to unparsed regions of space. The alternative view claims that the visual environment is parsed into different objects or perceptual groups (e.g. Prinzmetal, 1981; Duncan, 1984) and that attention is allocated to objects. Studies supporting the object-based approach are build on two predictions: First, it is relatively difficult not to be influenced by distracting information which belongs to the same object or group (Kramer & Jakobson, 1991; Baylis & Driver, 1992). Second, it is difficult to attend to different objects simultaneously (Baylis & Driver, 1993; Baylis, 1994).

4. Neuroanatomical and -physiological data of selective attention

4.1. Selective spatial attention: One master centre or many centres

Crick (1984) adopted the searchlight analogy of attention and proposed that the cerebral control over the attentional beam is located in the dorsal and the ventral thalamus. The latter structure includes the reticular complex, the ventral lateral geniculate nucleus, the zona incerta and the closely related peri-geniculate nucleus. Whereas Crick (1984) put forward a model that was based on a single thalamic centre of attentional control, other studies postulated that selective attention is a compound function following concerted interaction of various different centres (Mesulam, 1981; Rizzolatti et al., 1985; Posner & Petersen, 1990; Posner & Rothbart, 1998; Corbetta & Shulman, 1998).

Rizzolatti and his colleagues (1985) proposed a multi-centre model of selective spatial attention and suggested that each cerebral region which computes overt responses in space is also capable to produce covert attentional responses (see also

Corbetta & Shulman, 1998). The authors argued against the existence of a single attentional centre by pointing out that "a syndrome so severe and enduring as should occur after a lesion of any 'master' center" is lacking (Rizzolatti et al., 1985, p.262; see also Cubelli et al., 1991).

Mesulam (1981) presented the following integrated network for the modulation of directed attention consisting of four cerebral regions: The "posterior parietal component provides an internal sensory map"; ... "a limbic component in the cingulate gyrus regulates the spatial distribution of motivational valence; a frontal component co-ordinates the motor programs for exploration, scanning, reaching, and fixating; and a reticular component provides the underlying level of arousal and vigilance" (Mesulam, 1981, p.309).

Posner and Petersen (1990) also advocated a network of anatomical areas and specified further that this system maintained its own identity and was anatomically separate from cerebral information processing systems like the sensory or motor system. It was also postulated that the components of the network performed different functions and computations which could be expressed in cognitive terms. Three major computations of the attentional system were proposed to illustrate the functional subsystems of attention: First, orienting to sensory events; second, detecting signals for focal (conscious) processing; third, maintaining a vigilant or alert state. According to Posner and Petersen (1990) the function of orienting is associated with the parietal cortex wheareas the anterior cingulate appears to be particularly sensitive to target detection. The importance of the anterior cingulate has recently been re-emphasised and extended in imaging studies (Posner & Rothbart, 1998). It was shown that different areas of the cingulate structure are activated both during selection and error detection tasks. As for the ability to generate and sustain alertness, the norepinephrine system of the locus coeruleus in particular seemed to be crucial for alertness by acting on the parietal cortex to support visual orienting. Posner and Petersen (1990) stressed that this effect is greatest in the right hemisphere which is concordant with the view that the right hemisphere has a specialised function in the attention system (see also Mesulam, 1981). For example, in a positron emission tomography (PET) study, Pardo et al. (1991) demonstrated increases in blood flow in the prefrontal and superior parietal cortices mainly in the right

hemisphere. This effect persisted regardless of the modality or laterality of sensory input in a visual and somatosensory task of sustained attention. A similar asymmetry was revealed by Corbetta et al. (1993).

A series of different PET studies have provided evidence for a multi-centre/circuit system of attention. Corbetta et al. (1991) investigated the functional neuroanatomy with regard to selective and divided attention during visual discrimination of features like shape, colour and speed. The results showed that in the visual system, selective attention to different features modulates activity in specific areas of the extrastriate cortex that are specialised for the processing of the selected feature. More specifically, attention to speed activated the left inferior parietal lobule. Attention to colour increased uptake of the blood flow tracer in the region of the collateral sulcus and dorsolateral occipital cortex. Finally, attention to shape activated the collateral sulcus, fusiform and parahippocampal gyri and the temporal cortex along the superior temporal sulcus. Outside the visual system, activation of non-overlapping brain regions were activated by selective and divided attention. Conditions of selective attention activated the globus pallidus, caudate nucleus, lateral orbito-frontal cortex, posterior thalamus/colliculus and the insular pre-motor area, while divided attention activated the anterior cingulate and dorso-lateral pre-frontal cortex. Similar evidence for enhanced activity in different regions that are specialised for the computation of information related to the selected attribute were provided by a number of different studies (Roland, 1981; Corbetta et al., 1990; Haxby et al., 1994).

4.2. Neuronal mechanisms of selective attention

In the 'biased competition' model (Desimone et al., 1990; Desimone & Duncan, 1995; Desimone, 1998), selective attention "is best understood in the context of competition among all of the stimuli in the visual field for control over behaviour" (Desimone, 1998, p.1245). These competitive interactions between stimuli occur at the receptive field level and are influenced by two mechanisms rather than a single attentional control system: Bottom-up or stimulus-driven information (e.g. a higher contrast of one stimulus compared to a second one) and 'top-down' feedback mechanisms (e.g. greater behavioural relevance of one stimulus). Desimone (1998)

further speculated that the main source for top-down feedback is the pre-frontal cortex which has been associated with working memory (Courtney et al., 1998).
The role of top-down selective influences is to bias the processing at a cellular level towards one stimulus or the other. The physiological correlate of the bias appears to be an elevation of the neuronal baseline firing rates whenever attention is directed towards the neurons' receptive fields as it has been observed in V4 neurons (Luck et al., 1997) and the infero-temporal cortex (Chelazzi et al., 1993). The effect of elevated baseline firing rate has been documented both *before* a stimulus was shown to the receptive field or when no stimulus was presented at all (Luck et al., 1997).
It has been suggested that the neural firing bias might correspond to an attentional search template that specifies the relevant features of an object or a task. The bias signal "would be consistent with cognitive models of attention in which the selection of attended information is achieved by comparing incoming sensory information with an 'attentional template' " (Hillyard et al., 1998, p.1258). This definition places the 'biased competition' model within the category of effect theories.

Apart from the bias signal, a second attentional mechanism has been observed: The amplification of neuronal activity within sensory processing areas. Typically, the response of evoked potentials to a stimulus is larger when the stimulus appears in an attended region compared with an unattended location (Hillyard et al., 1998). Evoked potentials represent the summated electric field arising from populations of nerve cells activated by a stimulus. The amplitude of the neuronal signal is increasingly enhanced the more the response of the involved neuronal population is synchronised (Roelfsema et al., 1994; Singer, 1993). Therefore, synchronisation of neuronal activity, i.e. the temporal structure of the signal, has been proposed as a crucial process mediating attention (Singer, 1995, 1998).

To summarise, in this chapter we have presented the main theories of selective attention. Furthermore, neuroanatomical data and -physiological mechanisms of attention have been reviewed. In the next chapter, we will propose a new approach to unilateral neglect which builds on one of the neurophysiological mechanisms of attention presented above: Synchronisation of neuronal discharge.

Chapter Four

Unilateral neglect as temporal diplopia

1. Introduction

Halligan and Marshall (1992, p.533) have made a strong and clear claim: "Neglect is a meaningless entity". We agree. The range of possible anatomical lesions sites, the patterns of dissociations, the clinical differences between individual neglect patients make arguments in favour of a coherent neglect syndrome seem unconvincing (see also Stone et al., 1998). Halligan and Marshall (1992) furthermore questioned that one pathological mechanism will ever account for the whole spectrum of neglect symptoms but also continued by stressing the necessity of finding such underlying "principles" of malfunction (Halligan and Marshall, 1992, p.532). Concordant with the above view, the present study has set out to investigate one such principle.

In the following sections, we will present an approach to unilateral neglect that investigates impaired neuronal synchronisation as one potential pathological mechanism causing 'neglect symptoms'. Unilateral neglect has also been documented in connection with Alzheimer's disease (Ishiai et al., 1996; Bartolomeo et al., 1998; Venneri et al., 1998) and Parkinson's disease (Villardita et al., 1983; but see Brown & Marsden, 1986) but we will concentrate on the pathological mechanisms of stroke as most neglect patients present with lesions due to cerebrovascular accidents. We will begin the outline of the theory by discussing the patho-physiological changes after cerebrovascular trauma.

2. Patho-physiological changes after a cerebro-vascular accident

2.1. Introduction

Before any theorising about a neuropsychological impairment, one should be quite clear about the patho-physiological changes in the brain that occur after cerebral

trauma. We will concentrate here on the consequences of a cerebro-vascular accident which is the most commonly reported cause of unilateral neglect.

Cerebro-vascular accidents or strokes are a major health problem. In Scotland, about 4.5 % of all deaths among people under 65 years are caused by strokes. When all age groups are taken into account, stroke is associated with about 11.5 % of all deaths (Scottish Office Department of Health, 1998). Of those who do not die from the trauma, some 50% remain severely disabled (Anderson, 1985). Although there is a wide variety of measures and definitions of disability, disability statistics tend to rank stroke related disability as the largest single disabling condition (e.g. Glasgow City, Joint Community Care Plan, Consultation Draft, 1998). About 85% of strokes are caused by ischemic brain damage (cerebral infarction) while the remaining 15% are due to spontaneous intracranial bleeds (Anderson, 1985). The ensuing cerebral changes can be divided into focal and global changes of brain physiology.

2.2. Focal changes

Normal cerebral blood flow is approximately 50 ml per 100 g of brain tissue per minute (Aitkenhead & Smith, 1990). If infarct occurs, two areas of focal ischemia can normally be distinguished: One region, the core, where blood flow ranges between 0 to 20 ml per 100 g of brain tissue per minute and an intermediate area, the penumbra, where blood flow is of the order of 20 to 50 ml per 100 g of brain tissue per minute. The cerebral damage depends very much on the degree of blood flow reduction. If blood flow has been interrupted completely, the neurons of the affected region will be irrevocably damaged after approximately 5 minutes. With blood flows of as low as 10 ml per 100 g of brain tissue per minute, neurons might be viable for up to an hour (Sharp et al., 1998). These figures refer to gray matter damage. White matter has generally been considered less vulnerable to ischemia than gray matter but there is recent evidence for a similarly high vulnerability of white matter to ischemia (Pantoni et al., 1996).

The primary effect of ischemia is decreased supply of oxygen and glucose, substrates which are vital for the normal neuronal energy metabolism. Another primary effect is the reduced removal of lactate. Lactate builds up due to the anaerobic metabolism of

glucose to produce 2 ATP instead of 36 ATP normally generated by aerobic metabolism (Krebs cycle). This build-up of lactate leads to a drop of the normal pH of 7.0. A reduced pH of 5.9 is known to result in tissue infarction. Secondary effects of ischemia include release of excitatory neurotransmitters, increase of intracellular calcium, activation of proteases and lipases, the release of free radicals, the activation of intracellular second messengers and the induction of genes that promote cell death. Depending on the severity of ischemia, the combination of these factors can either lead to pan-necrosis or selective necrosis. In pan-necrosis, the combined death of all cellular elements, including neurons, glia and endothelial cells are found. In selective necrosis, only the neuronal population is involved in cell death (Sharp et al., 1998).

So far only focal changes after ischemic lesions have been considered. However, the mechanisms of damage are similar after rupture of a cerebral blood vessel since the tissue which it supplies is subsequently starved of blood. In addition, bleeds are space occupying lesions that can cause severe macrological destruction with a rapid increase in intracranial pressure (Anderson, 1985).

In the next section, we will illustrate that focal lesion does not necessarily equal focal damage. Widespread global cerebral changes have been shown to be a consequence of focal injury.

2.3. Global changes and diaschisis

After focal cerebral damage there are widespread changes affecting the cerebral blood flow (Olsen et al., 1981; Celisia et al., 1984), the metabolic rate (Metter et al., 1986) and electrophysiological activity (Obeso et al., 1980; Jordan, 1993) of the damaged and the undamaged hemisphere (Andrews, 1991; Buchkremer-Ratzmann et al., 1996). However, although the involvement of the contralesional hemisphere can frequently be found, the degree of decreased blood flow, metabolic rate and the electrophysiological changes of the contralesional side are not as severe as in the affected hemisphere (Celesia et al., 1984; Fiorelli et al., 1991; Perani et al., 1993).

The concept of "diaschisis", first coined by von Monakow (1914a), describes specific acute or subacute changes of cerebral areas which are remote from the primary locus

of cerebral damage: "... diaschisis represents an 'interruption of function' appearing in most cases quite suddenly ... which originates from a local lesion but has its point of impact not in the whole cortex (corona radiata etc.) like apoplectic shock but only at points where fibres coming from the injured area enter into primary intact gray matter of the whole central nervous system " (von Monakow, 1914b; quoted by Andrews, 1991).

Von Monakow (1914) distinguished different types of functional dissociation whose assumed mechanism was loss of excitation to intact regions rather than neural inhibition: Diaschisis cortico-spinalis (decreased function between motor cortex along the pyramidal tract), diaschisis commissuralis (impaired function of the contralesional hemisphere) and diaschisis associativa which described impairment spreading along associative fibres within one hemisphere (Feeney & Baron, 1986). More recently, Baron et al. (1980) proposed a further form of diaschisis which describes functional changes in the contralesional cerebellum.

Only during the last few decades technological development allowed the scientific examination of diaschisis. Investigators of the theory were studying the remote effects of lesions by examining neurotransmitter levels, synaptic receptors, electrophysiological activity, cerebral metabolism and blood flow (Feeney & Baron, 1986).

Original techniques to measure cerebral blood flow and metabolic rate used intracarotid injections of radioactive tracers. More recently, less invasive techniques like positron emission tomorgraphy (PET) and single photon emission computerised tomography (SPECT) have been developed.

A series of studies has demonstrated that cerebral blood flow is decreased throughout the injured and contralesional hemisphere after unilateral cerebral trauma (Høedth-Rasmussen & Skinhøj, 1964; Skinhøj, 1965; Meyer et al., 1970; Slater et al., 1977; Celesia et al., 1984; Takano et al., 1985; Lagrèze et al., 1987; Perani et al., 1987; Bogousslavsky et al., 1988; De Weerd et al., 1988; Dobkin et al., 1989). Although hyperemia, i.e. increased perfusion, can be observed in the acute state (within the first two days) (Olsen et al., 1981), decreased perfusion is prevalent in the acute, subacute (two to ten days after the stroke) and chronic stages (more than 30 days

after the cerebral trauma) (Celesia et al., 1984). Vallar et al. (1988) demonstrated a decreased perfusion rate of the affected hemisphere at an average of 3.2 months after onset of stroke in 20% of the subcortical patient group. De Weerd et al. (1988) measured cerebral blood flow in unilaterally damaged patients over three years. It was reported that at the three year mark 30% of the patients still had abnormal blood flow patterns over the affected area. Furthermore, the results also showed that the cerebral blood flow of the damaged hemisphere deteriorated in 25% of the patients during the three years of observation. Blood flows in the non-affected hemisphere were slightly but not significantly higher than in the injured hemisphere.

Perani et al. (1987) examined a group of 16 patients who had suffered unilateral subcortical strokes. The results suggested that a more pronounced decrease of cortical cerebral blood flow is associated with neuropsychological deficits like aphasia and neglect (see also Olsen et al., 1986).

There are some methodological problems with the measurement of cerebral blood flow. For example the arterial pressure of CO_2 (P_{aCO_2}) or the hematokrit can be confounding physiological variables that make the metabolic rate a preferable measure of functional change (Iglesias et al., 1996). Furthermore, cerebral perfusion and metabolism can be dissociated under certain circumstances (Fieschi, 1980; Wise et al., 1983).

There are numerous studies documenting metabolic depression of cerebral areas in both hemispheres remote from the area of acute neuronal damage (Lenzi et al., 1982; Wise et al., 1983; Metter et al., 1986; Kiyosawa et al., 1990; Fiorelli et al., 1991; Baron et al., 1992; Perani et al., 1993; Iglesias et al., 1996). Perani et al. (1993) investigated the acute and chronic stages of cerebral metabolism after unilateral cerebral damage in a couple of single case studies. The first patient showed bilateral reduction of the metabolic rate as late as at four months after admission. A second patient was examined at six months after she had suffered the initial trauma. It was shown that reduced metabolism was still present in the affected hemisphere whereas the metabolic rate had returned to normal values in the contralesional hemisphere.

In his model of cerebral glucose metabolism, Sokoloff (1977, p.25) investigated the relationship between the physiological function of the cerebral tissue and the energy

metabolism in the central nervous system. He stated quite clearly: "Functional activity in specific components of the CNS is, as in the other tissues, closely coupled to the local rate of energy metabolism".

To summarise, we have demonstrated that there is ample evidence for reduced metabolic activity both in the affected and unaffected hemispheres. Sokoloff (1977) has emphasised the strong relationship between cerebral metabolism and functional integrity. The next question we would like to ask is what is the neurophysiological correlate of the impaired neuronal energy metabolism? Before we give a tentative answer to this question we will turn to the electrophysiological changes that are observed after unilateral cerebral damage.

3. Slowing down of neuronal processing as a correlate of global changes

Electro-encephalography (EEG) is the representation of the spatial and temporal summation of cortical postsynaptic excitatory and inhibitory potentials. The EEG is the composite picture of complex intracellular, interneuronal and neuronal-glial activity and therefore a sensitive measure of cerebral metabolism (Jordan, 1993).

There are different frequency ranges found in a human EEG. The delta band (0.5 to 4 Hz) is recorded during slow wave sleep, but also during pathological states like ischemia, anaesthesia and coma. The theta band (6 to 7 Hz) is recorded in healthy limbic structures, during ischemia of the brain, in the hippocampus and the entorhinal cortex during attentive arousal. Activity in the alpha range (around 10 Hz) is correlated with states of drowsiness and relaxation, whereas the beta (15 to 30 Hz) and gamma bands (30 to 60 Hz) are recorded during focused attention (Singer, 1993). Paradoxically, during states of alertness and arousal the EEG pattern is referred to as a 'desynchronised' state because the EEG shows a broad range of frequencies between 10 to 60 Hz. Traditionally, it was assumed that this pattern is due to temporally incoherent activity of spatially distributed neurons. However, refined methods of measurement have demonstrated that fast synchronisation is significantly enhanced when the EEG is in a so-called 'desynchronised' state (Munk et al., 1996; Steriade et al., 1996).

Since Berger (1934) first reported the appearance of slow waves in cerebral hypoxia, a wealth of studies have investigated the correlation of clinical data in cerebro-vascular disease and EEG recordings. Berger's first description of delta and theta waves, i.e. the presence of slowing of neuronal activity after stroke, has been confirmed in numerous studies (e.g. Marquardsen & Harvald, 1964; Ladurner et al., 1972; Hammond et al., 1982; MacDonell et al., 1988; Giaquinto et al., 1994). The EEG has been used to identify circumscribed areas of focal slow activity and generalised slowing of background activity.

Meyer et al., (1970) reported that in some patients the EEG showed intermittent slowing involving both hemispheres. It was not specified how many patients displayed these EEG patterns, though. Melamed et al. (1975) examined 22 patients with acute unilateral cerebral damage. Out of the entire group, 19 of the patients showed EEG slowing over the infarcted hemisphere and six patients also suffered from slowing over the contralesional hemisphere. Tohgi (1977) demonstrated that large infarcts can cause bilateral symmetrical slow waves in the acute stage of injury. Jordan (1990) performed continuous EEG monitoring in patients with acute cerebral ischemia and reported that the EEG's in 45% of the patients showed worsening of focal slow activity, appearance of epileptiform activity or the development of generalised slowing over both hemispheres. A different study that examined 79 patients with unilateral ischemic lesions found a significant correlation between background slowing and the level of consciousness. At two days after admission, 21 patients of the 32 patients with disturbed consciousness showed general background slowing. In the group of 45 patients with full consciousness, only twelve patients displayed theta and delta activity (Kayser-Gatchalian & Neundörfer, 1980).

On the other hand, Sainio et al. (1983) reported that, at four weeks after infarct, 45% of the patients still showed abnormal background activity in the EEG. This measurement referred to the EEG recorded on the day of discharge which means that the patient group cannot have suffered large infarcts and yet the rate of EEG background abnormality was 45%. Sainio et al. (1983) claimed that the level of consciousness had been impaired in only one patient on the day of admission. De Weerd et al. (1988) reported that out of a group of 40 unilateral patients, twelve

patients still showed abnormalities in the overall frequencies over both hemispheres three years after cerebral damage.

The recording of evoked potentials is a different method to measure electrophysiological activity of the brain. Evoked potentials, like the EEG, are correlated with the metabolic rate of the brain but they appear, however, to be much more resistant to metabolic and perfusion changes (Jordan, 1993). Branston et al. (1974) demonstrated in an animal model that the somato-sensory evoked potentials (SEP's) were not affected at blood flows greater than 16 ml/100 g/min but they were abolished at levels below 12 ml/100 g/min. Usually, absence of SEP's over the infarcted hemisphere is a predictor of irreversible neurological impairment (Chiappa & Hoch, 1993).
Data on evoked potentials in stroke patients are not unequivocal. Nakashami et al. (1985) reported either normal or increased SEP's over the non-affected hemisphere of stroke patients. Obeso et al. (1980) demonstrated both increased duration and amplitude of SEP's over both hemispheres but mainly over the damaged hemisphere. Vallar et al. (1991) reported normal SEP's in the stroke group who displayed neglect. However, Spinelli et al. (1994) demonstrated normal amplitudes of visual evoked potentials (VEP's) in the right hemisphere group but recorded increased latencies to contralesional stimulation only in patients who suffered from neglect. Spinelli et al. (1994) attributed the discrepancy with Vallar et al.'s (1991) results to the use of refined technical methods in their own study.

To summarise, EEG studies have repeatedly demonstrated both focal and general background changes of electrophysiological activity after cerebro-vascular accidents. Slow delta and theta waves have been documented both over the affected and the intact hemisphere in a significant number of unilateral hemisphere patients. Evidence from evoked potential experiments is not as clear. However, Jordan (1994) has emphasised that evoked potentials are not the most sensitive measure of functional impairment after ischemic damage. There are also some technical caveats to this method (Spinelli et al., 1994). Furthermore, the recording of the evoked potential represents only a minimal aspect of the spatio-temporal continuum from the entire

cerebral electrophysiological activity (Petsche & Rappelsberger, 1992) and, compared to the EEG, is therefore less likely to capture changes.

We will therefore conclude that general slowing down of neuronal activity is a neurophysiological correlate of stroke. Henceforth, this conclusion will be applied as a working principle.

4. Synchronicity, induced rhythms and the encoding problem

Studies using different techniques ranging from single/multi-unit and local field potential to EEG recordings have demonstrated that synchronous activity is a widespread phenomenon in the vertebrate and human brain (Bullock, 1992; Gray, 1994).

Synchronous discharge can occur as a single event or in a repetitive periodic way. In the latter case, the product of synchronicity are oscillations. When the interval between successive bursts is long, low frequency oscillations are generated. High frequency oscillations are the consequence of short burst intervals. The amplitude of the oscillatory field potential appears to decrease when the frequency increases. This observation suggests that fewer neurons are involved in rapidly oscillating neuronal assemblies (Singer, 1993).

There are three different classes of oscillations that have to be distinguished: Induced rhythms, driven oscillations and spontaneous oscillations. Induced rhythms are oscillations that are caused or modulated by stimuli or state changes. These stimulus-related rhythms are self-generated and non-phased locked to the stimulus, i.e. they appear after a latency with respect to the stimulus onset. Although they are triggered by an external stimulus, their temporal structure is mainly influenced by interactions within the participating neuronal populations. Driven oscillations, on the other hand, are phase-locked and correlated with the stimulus which directly drives the oscillatory activity. The third class of rhythmic activity is spontaneously occurring rhythms (Bullock, 1992; Singer, 1999).

It is the first category of oscillations, induced rhythms, that has received increasing attention during the last 20 years (for a review see Basar & Bullock, 1992; Aertsen & Arndt, 1993). Induced rhythms are of particular interest because their characteristic

response patterns suggest that aspects of neuronal processing may be independent of the properties of the stimulus per se. Induced rhythms have been discussed in connection with both primary sensory processes and cognition (Von der Malsburg, 1981; Von der Malsburg & Schneider, 1986; Crick & Koch, 1990; Bressler et al., 1993; Singer, 1993; Tiitinen et al., 1993; Joliot et al., 1994; Pfurtscheller et al., 1994; Pulvermüller et al., 1996; Tallon-Baudry et al., 1997; Miltner et al., 1999; Rodriguez et al., 1999; Singer et al., 1999).

It has to be emphasised that although synchronisation and oscillatory activity often occur together, they are not necessarily associated with each other (König et al., 1995). The absence of oscillations does not exclude synchronicity and vice versa. In the former case, two cells could always discharge simultaneously but at irregular intervals. On the other hand, single neurons can engage in oscillatory activity without being synchronised with other cells. Furthermore, absence of oscillations or synchronicity are no proof of their non-existence. For example, oscillatory phenomena in the brain are so irregular that auto-correlation functions obtained over prolonged periods of time often fail to show the oscillatory patterns of the underlying time series. However, it has been suggested that oscillations are a likely consequence of synchrony and that they might be the prerequisite to establish synchrony over large distances across cerebral structures (Singer, 1993, 1995).

To summarise, we have established that synchronous activity is a widespread phenomenon. Furthermore, we have postulated in the previous section that focal cerebral damage can slow down synchronous discharge. We will now discuss the possible function of synchronous activity in the human brain and will then describe the potential consequences of impaired synchronicity for perceptual and cognitive processing after focal cerebral injury.

4.1. The binding and superposition problem

It is unquestioned that synchronicity is of crucial importance for signal transmission and neural plasticity. The timing of afferent activity is all-important because, first, synaptic discharge is of finite duration and, second, because the firing threshold of the receiving neuron has to be reached. By synchronising afferent activity a

summation effect will be achieved. Also, the degree of synaptic modification between two neurons depends on the level of post-synaptic depolarisation and thus on the accuracy of synchronised activity (Singer, 1993). However, whether synchronisation is an important mechanism for information encoding and cognitive processing is still debated (Ghose & Freeman, 1992; Tovée & Rolls, 1992; Shadlen & Newsome, 1994; Golledge et al., 1996; Hardcastle, 1997; Lamme & Spekreijse, 1997).

The human visual system is characterised by an almost infinite capacity to recognise patterns and objects. How has the visual system mastered coping with the enormous combinatorial stimulus potential that the visual world holds for it? To detect and recognise an object within a scene, the features of this object have to analysed and segregated from features belonging to different objects (Singer & Gray, 1995).
Traditionally, it was thought that a system of neurons in the sensory part of the brain, so-called feature-detectors, operated at different levels. On the lowest level, a feature detector responds to the activation of a single sensory cell. On the most central level, feature detectors represent entire objects. These central feature detectors have also been termed cardinal cells (Von der Malsburg, 1981). Figure 1 illustrates this organisational principle.

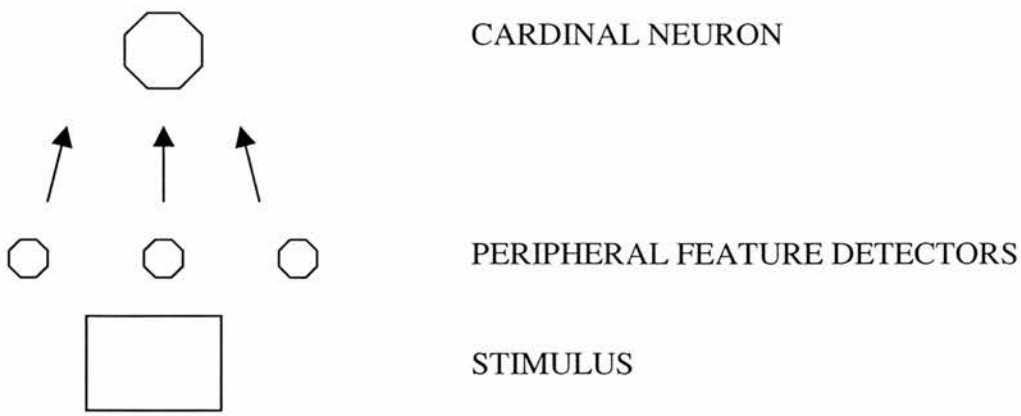

Fig. 1: Three peripheral feature detectors encode features like colour, shape and size.

The traditional view held that information from the peripheral feature detectors is couched in a rate code, i.e. by the number of times a neuron fires in a given time

interval. This was based on the observation that the firing rate of peripheral nerves was correlated with the amount of sensory stimulation (Adrian, 1928). A second postulate was the principle of convergence. The peripheral feature detectors converge their information onto one central cardinal cell. However, if we look at figure 2, it becomes clear that this system will soon run into a number problem.

Fig. 2: Two different stimuli are encoded in two different neuronal sets.

The system in figure 2 would need a cardinal neuron for the representation of every stimulus that has ever been presented to the visual system. Furthermore, there should be an infinite number of cardinal neurons as yet unassigned for every potential *new* stimulus that might appear in the future. It is obvious that this system would be highly uneconomical. The number problem could be mitigated if there were more convergence. However, as figure 3 illustrates, if there is too much convergence, ambiguities soon arise.

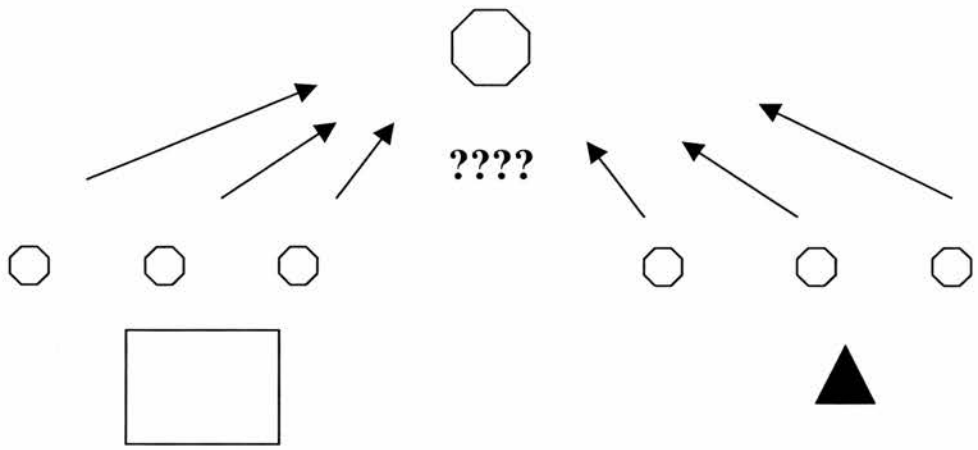

Fig.3: Two different stimuli are encoded by one cardinal neuron. Too much convergence generates ambiguities in the assignment of specific features to the correct stimulus.

However, even if there were an infinite number of cardinal neurons available to the system, it would not be possible to solve the processing problem that arises in figure 4. How could the system bind together all the features that belong to each stimulus when both stimuli are superimposed? This situation refers to the binding and superposition problem.

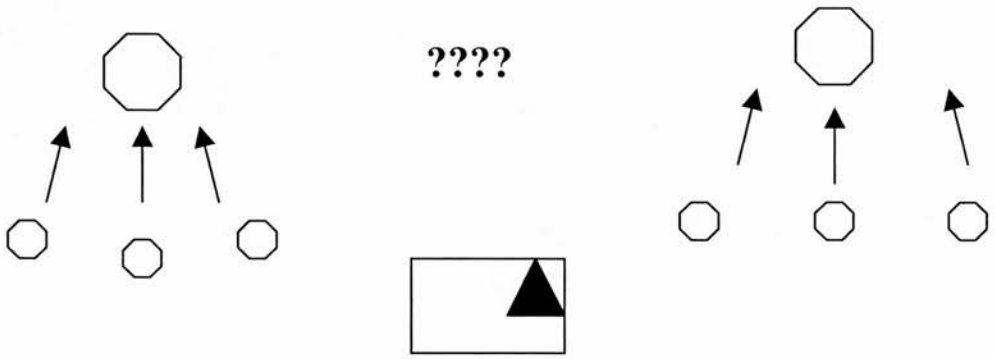

Fig. 4: The binding and superposition problem: The two sets of neurons can not represent two superimposed stimuli unambiguously.

For the above reasons and because of the fact that so far no object-specific cardinal neurons have been found, apart from neurons encoding features of faces and hands (Perrett et al., 1987; Rolls, 1991), a different theoretical approach has been proposed. While maintaining the principle of convergence, two alternative processing mechanisms have been postulated in the encoding of sensory information: First, assembly coding as opposed to single neuron coding and, second, an encoding strategy that is couched in the temporal signatures of the neuronal firing patterns as opposed to a rate code only. This new concept has been referred to as the temporal correlation hypothesis (Von der Malsburg, 1981; Von der Malsburg & Schneider, 1986; Singer et al., 1990; Singer, 1993, 1995; Singer & Gray, 1995; Engel et al., 1992, 1997).

4.2. Synchronicity and the temporal correlation hypothesis

Assembly coding has been proposed as an alternative mechanism because the number of cells that are necessary to represent different patterns would be reduced significantly, be it at a peripheral or central level. This system would allow for much greater flexibility in the generation of new representations. The great advantage of

assembly coding is that individual cells can be involved in the representation of different objects at different times (Singer, 1993, 1998; Singer & Gray, 1995; deCharms & Merzenich, 1996; Sakurai 1996, 1998; Roelfsema, 1998). "The assumption is that just as a particular feature can be present in many different patterns, the group of cells coding for this feature can be shared by many different representations in that they participate at different times in different assemblies of co-active neurons. The code is thus relational and the significance of an individual response depends entirely on the context set by other members of the assembly" (Singer & Gray, 1995, p.558).

To take full advantage of assembly coding, mechanisms are necessary to ensure the flexible and unambiguous association of neuronal activity. Therefore, synchronisation of neuronal discharge with a precision in the millisecond range has been proposed as the required strategy to represent relationships among neurons with very high accuracy (Von der Malsburg, 1981; Singer, 1993, 1998; Singer & Gray, 1995). A slightly modified version of this approach is the postulate of synchronisation in conjunction with the principles of the rate code (Roelfsema et al., 1996).

Furthermore, if synchronous activity is generated quickly and maintained for only a brief time period, a set of different neuronal populations can be established in rapid temporal succession (Singer, 1990; Eckhorn et al., 1992; Singer, 1993; Singer & Gray, 1995; Roelfsema et al., 1996).

Most of the synchronisation studies have been conducted with animals but research in this field has increasingly involved human subjects (Tiitinen et al., 1993; Desmedt & Tomberg, 1994; Joliot et al., 1994; Pantev, 1995; Tallon-Baudry, 1997; Miltner et al., 1999; Singer, 1999; Rodriguez et al., 1999).

A lot of attention has been focused on synchronised activity in the gamma frequency range from 30 to 60 Hz which has been suggested as an appropriate band width to fulfil the above processing requirements (Llinás & Ribary, 1992; Singer, 1993; Desmedt & Tomberg, 1994; Joliot et al., 1994; Pantev, 1995; Singer & Gray, 1995; Muller et al., 1997; Tallon-Baudry, 1997; Miltner et al., 1999; Singer, 1999;

Rodriguez et al., 1999). Psychophysical studies have demonstrated that a natural scene is segmented by the visual system within 100 to 200 ms (Burr, 1981; Biedermann, 1990). Oscillations in the alpha and beta range would be too slow to achieve the required speed of encoding. On the other hand, oscillations must not be too quick in order to allow for long-range synchronisation with zero-phase lag between different neuronal populations, as has been demonstrated (e.g. Roelfsema et al., 1997). Thus gamma band activity appears to be a good solution to the above mentioned neurophysiological constraints (Singer, 1993; König et al., 1995).

Different sites of synchronous firing have been documented: Synchronisation between populations inside a cortical column (e.g. Eckhorn et al., 1988, 1992), between cortical columns (Gray et al., 1989b; Engel et al., 1990; Schwarz & Bolz, 1991), and between near (e.g. Eckhorn et al., 1988, 1992) and far cortical areas via long-range connections (Traub et al., 1996; Rodriguez et al., 1999; Miltner et al., 1999) including interhemispheric fibres (Engel et al., 1991; König et al., 1995). Every cortical area can be involved in synchronous discharge (Bressler et al., 1993; Tiitinen et al., 1993; Miltner et al., 1999; Rodriguez et al., 1999). Llinás et al. (1998) have also stressed the importance of thalamo-cortical connections in synchronised activity as opposed to synchrony mediated by cortico-cortical fibres (e.g. Singer, 1998).

It has been postulated that the probabilities with which distributed cells synchronise their responses are correlated with Gestalt criteria of perceptual grouping (Koffka, 1935): Proximity, similarity, continuity and common fate (Singer, 1993, 1995, 1998; Singer & Gray, 1995; Roelfsema et al., 1996). These principles reflect the fact that objects are formed by features that are grouped together in close proximity, that share properties like form and colour, that are spatially contiguous to each other and finally, when they move, they move into the same direction.
Studies of the animal visual system have provided evidence that synchronous activity spreads across neighbouring receptive fields as a direct response to spatial stimulus properties (Roelfsema et al., 1996). The synchronisation pattern is more likely to involve neuronal assemblies that encode the same stimulus properties, like form

(Engel et al., 1991b) or colour (Ts'o & Gilbert, 1988). Support for the continuity principle came from a study by Schwarz and Bolz (1991). It was demonstrated that the probability of detecting intercolumnar synchronisation was greatest not only when the cells had similar orientation preferences but also when the receptive fields of the neurons were in a collinear configuration. As for the criterion of common fate, Engel et al. (1991c) measured the synchronous activity of cells with non-overlapping receptive fields and similar orientation preference. No synchronicity was found when two contours were moved in opposite directions across the receptive fields. The correlation was weak but significant for two bars moving in the same direction. The strongest response was elicited by a single bar moving over both fields. Furthermore, if neuronal assemblies with overlapping receptive fields but different orientation preferences are stimulated by a single moving bar, the different groups synchronise their activity even when some sub-populations are not optimally stimulated. If, however, the same set of neuron populations is activated by two different objects moving in opposite directions, they no longer establish one simultaneously active group but form two independent synchronised assemblies (Engel et al., 1991b).

Recently, evidence has been produced for the claim that synchronous activity is also a crucial mechanism for cognition - not only for primary sensory processing. Synchronised neuronal activity in humans has been reported in connection with motor tasks (Pfurtscheller et al., 1994), a somato-sensory task (Desmedt & Tomberg, 1994), a lexical decision task (Pulvermüller et al., 1996) and with a visual search task (Tallon-Baudry et al., 1997).

Rodriguez et al. (1999) recorded the EEG in human subjects during a face recognition paradigm. The subjects were required to press a button to indicate their response to the stimuli. Strong synchronous activity was found during the recognition of a face compared to the non-face condition. A subsequent period of strong desynchronisation indicated the transition between the moment of perception and the motor response. Rodriguez et al. (1999, p.431) concluded that "desynchronisation reflects a process of active uncoupling of the underlying neural ensembles that is necessary to proceed from one cognitive state to another" (see also Pfurtscheller & Klimesch, 1992).

Miltner et al. (1999) provided evidence for a connection between synchronicity and associative learning. In a classical conditioning paradigm during which the EEG activity was recorded, the subject gradually learned to associate a weak electric shock with a particular colour. Miltner et al. (1999) demonstrated not only an increase of synchronicity in the occipital and parietal electrode sites in response to the conditioning procedure but the authors also showed that synchronous discharge developed *between* the visual and the pericentral/posterior parietal somato-sensory association area during the associative learning phase.

Memory, attentional processes and consciousness have also been discussed in connection with synchronised activity (Crick & Koch, 1990; Tononi et al., 1992; Eckhorn et al., 1992; Kinsbourne, 1993b; Tiitinen et al., 1993; Pöppel, 1993; Pöppel & Schwender, 1994; Desmedt & Tomberg, 1995; König & Engel, 1995; Singer, 1995, 1998; Llinás et al., 1998).

König and Engel (1995) reviewed the literature on the relationship between synchronous activity and the hippocampal formation which has been attributed a crucial role in memory and retrieval (Mishkin, 1995). Bragin et al. (1995) have demonstrated synchronous discharge of the gamma and theta range in the hippocampus. Furthermore, neural network studies have successfully used oscillatory elements to simulate hippocampal function (Wang et al., 1990; Ritz et al., 1994; Sompolinsky & Tsodyks, 1994).

Crick and Koch (1990) have presented a model that associated synchronous activity with attention and consciousness. The authors postulated that "40-Hz oscillations are the neural correlate of vivid visual awareness" (Crick & Koch, 1990, p.954). According to this model, a spotlight which is controlled by a saliency map selects the representations of the most salient objects in several cortical areas and boosts the 40-Hz oscillations encoding these objects. A saliency map (Koch & Ullman, 1985) is a representation of where salient objects are and not which objects are salient. According to Crick and Koch (1990), the most likely storage site of saliency maps are the pulvinar, the thalamic reticular nucleus and the posterior parietal cortex (Crick & Koch, 1990). Tiitinen et al. (1993) provided support for this model by showing that 40-Hz oscillations following an auditory stimulus were enhanced when this stimulus had been attended to by the subject. Roelfsema et al. (1997)

demonstrated attention-related facilitation of synchronisation in cats that had been trained to perform a motor task in response to certain stimuli. The authors reported synchronisation without time lag between areas of the visual and parietal cortices and between areas of the parietal and motor cortices when the cats responded to a sudden change of visual cues. During the inter-trial episodes the synchrony was lost.

Singer (1998, p.1834) proposed that "attentional mechanisms could impose a coherent sub-threshold modulation on neurons in cortical areas that need to participate in the execution of the anticipated task, thereby permitting the rapid synchronisation of selected responses". Furthermore, "shifts of attention across different modalities could be achieved by selectively enhancing synchronisation probability in particular sensory areas and not in others" (Singer,1995, p.120). Singer (1998) argued that attentional processes might be intrinsically linked with consciousness and proposed synchronisation as the substrate for awareness. Integration of representations on various processing levels, from the periphery to the centre, might be achieved by 'nesting' of oscillatory frequencies. The frequency of the oscillations tends to decrease as one proceeds from low to higher processing levels. Cell assemblies from different levels can have a small fraction of their discharge synchronised even if they oscillate at different frequencies (Castelo-Branco et al., 1998).

A different model has been put forward by Llinás et al. (1998). Unlike Singer (1998) who emphasised the cortex as the main site for the representation of synchronicity, Llinás et al. (1998) have proposed thalamo-cortical interconnectivity as the most important substrate for synchronised activity. According to this model, the thalamus is a central relay station from which any site of the cortex con communicate with any other cortical site through the interaction of thalamo-cortical loops. Llinás et al. (1998) have therefore postulated that the thalamus assumes a crucial function for cognition and consciousness by establishing synchronised connections with cortical areas.

The temporal correlation theory is not uncontroversial. Ghose and Freeman (1992) studied oscillatory discharge of neurons in the visual system of cats. The recorded oscillations did not show any relationship with the stimulus properties. Also, the

oscillatory discharge was described as unstable. It was concluded that "the oscillatory activity of single cortical neurons does not reflect parameters of patterned visual stimulation and may be an epiphenomenon of no obvious functional significance to the visual system" (Ghose & Freeman, 1992, p.1558). Tovée and Rolls (1992) failed to find a correlation between oscillations and the representation of static stimuli in their animal study (but see Neuenschwander & Singer, 1996). Similarly, Lamme and Spekreijse (1997) argued against a functional role of neuronal synchrony in texture segregation. However, numerous studies, including neural network models (Wang & Terman, 1997; Wennekers & Palm, 1999), have provided support for the claim that synchronisation is correlated with stimulus properties and that it is of functional importance in visual scene segmentation (Engel et al., 1989, 1990, 1991, 1991b,c; Gray & Singer 1989; Gray et al., 1990; Singer, 1993; Kreiter & Singer, 1994, 1996; Singer & Gray, 1995; deCharms & Merzenich, 1996; Gray & Di Prisco, 1997; Fries et al., 1997).

Hardcastle (1997) assumed a position against the significance of synchronisation by pointing out that the gamma band oscillations are attenuated during slow-wave sleep although consciousness does not seem to be extinguished during all stages of sleep (Hobson, 1988). Indeed, it appears that gamma band activity is reduced in slow-wave sleep (Llinás & Ribary, 1993). However, it is not completely removed from the observed frequency range (Maloney et al., 1997). Furthermore, oscillatory peaks in the alpha range (9 to 10 Hz) have been observed during slow-wave sleep (0.05 to 2.88 Hz) (Achermann & Borberly, 1998) which could indicate some encoding processes, only mediated by slower frequency bands. Conscious processing might be preserved during slow-wave sleep (Hardcastle, 1997) but nobody will question that the level of alertness is reduced. Therefore, a decrease of very fast oscillations is not too surprising.

According to Hardcastle (1997), a further argument against synchronisation is the fact that fast oscillations are maintained during anaesthesia. Hardcastle's objection is not valid since the recording of oscillatory activity in anaesthetised animals is a commonly used technique (e.g. Gray et al., 1992; Roelfsema et al., 1994; deCharms & Merzenich, 1996; Castelo-Branco et al., 1998). More importantly, the depth of anaesthesia had not been established in the study by Steriade et al. (1996) which

Hardcastle (1997) referred to. Furthermore, even if blood pressure and heart rate had been monitored during the study as is clinical practice but had not been reported, there is evidence that these measures are not correlated with the depth of the general anaesthesia and that instead evoked potentials should be recorded (Sebel et al., 1988). Therefore, no conclusions can be drawn from the occurrence of oscillations during anaesthesia in this case.

On a neurophysiological level, two prerequisites must be fulfilled for a synchronised processing system to work: First, neurons must function as coincidence detectors, i.e. they have to be able to compute coincident synaptic input. Second, neuronal populations have to establish fast and context-dependent synchrony of their distributed discharge. The first requirement is still controversial. If neuronal integration time of synaptic input is short compared to the mean interspike interval, coincidence detection is possible. If, however, the integration time is long, a summation of synaptic events over extended intervals is performed, i.e. the neuron acts as a temporal integrator. While Shadlen and Newsome (1994, 1995; see also Golledge et al., 1996) have argued in favour of a rate/integrator code which is propagated in a noisy neuronal environment, others (Abeles, 1982; Softky & Koch, 1993; Softky, 1994, 1995; König et al., 1996; Stevens & Zador, 1998) have suggested temporal coincidence as a conceivable encoding mechanism. The issue remains unresolved at this stage.
As for the second processing prerequisite, the rapid and context-dependent co-ordination of distributed discharge, evidence has been produced recently for fast long-range synchronisation with near zero-time lag between cortical areas (König et al., 1995, 1995 b; Neuenschwander & Singer, 1996; Roelfsema et al., 1997) which suggests that neurons are able to respond to input on a tightly defined time scale.

A different team (Golledge et al., 1996) has based its opposition to synchronisation as an encoding mechanism on neurophysiological studies demonstrating that the major part of information is conveyed by the neurons within the first 50 ms. In other words, object perception is possible in less than 50 ms (Tovée et al., 1993; Tovée, 1994; Tovée & Rolls, 1995). Golledge et al. (1996) continued to argue that stimulus-

dependent oscillations are not locked to stimulus onset. A significant increase of synchrony occurs around 200 to 300 ms after the presentation of the stimulus (Rodriguez et al., 1999). Thus, "for synchronization to provide a binding mechanism, it would have to occur very close to the stimulus onset" (Golledge et al., 1996, p.1093). However, Golledge et al. (1996) failed to elaborate this point further. It is not clear why the oscillatory activity should have to be locked to the stimulus onset as long as the information is conveyed eventually during the first 50 ms of neuronal activity. Furthermore, psychophysical studies have indicated that scene segmentation and feature binding of complex objects can be achieved within 100 to 200 ms (Burr, 1981; Biedermann, 1990) which would be more or less reconcilable with a synchronisation onset delay of 200 ms including the first 50 ms required to convey the majority of information.

In summary, the principles of the temporal correlation hypothesis have postulated synchronicity as an economic, flexible and unambiguous mechanism which is self-organising and mediated by a network of cortico-cortical (Singer & Gray, 1995; Singer, 1998) and thalamo-cortical connections (Llinás et al., 1998). Distributed groups of co-active neurons that encode a particular feature, or more centrally a set of features belonging to a perceptual object, are identifiable as members of a neuronal assembly because their responses were synchronised during a brief moment in time. In other words, synchronicity is used as a tagging device (Von der Malsburg, 1981; Crick & Koch, 1990; Singer et al., 1990; Eckhorn et al., 1992; Singer, 1993; Singer & Gray, 1995; Singer, 1998). Furthermore, recent evidence has suggested that the same encoding principles might apply to cognitive processes (Tiitinen et al., 1993; Desmedt & Tomberg, 1994; Joliot et al., 1994; Pantev, 1995; Tallon-Baudry, 1997; Miltner et al., 1999; Singer, 1998, 1999; Rodriguez et al., 1999).
Studies providing evidence against the temporal correlation theory have so far failed to produce unequivocal results. On the other hand, data in favour of the theory have also only been of an indirect nature and there is still no conclusive theory on the structure of neuronal representation. However, there is mounting evidence that synchrony might be of crucial significance for normal neuronal processing. We will therefore accept the principles of the temporal correlation theory as a feasible model

of neuronal encoding. Consequently, it is postulated that the disruption of synchronous activity can lead to the impairment of both primary sensory and cognitive processes.

Before discussing neglect in this framework, we will corroborate the above postulate by presenting strabismus, i.e. squint, and the phenomenon of binocular rivalry as examples of the potential correlation between decrease in synchronicity and the impairment of sensory processing.

5. Strabismus and binocular rivalry

Ideally, the visual axes of both eyes are aligned in parallel in distance fixation and have the appropriate convergence in near vision. Although in most people this kind of perfect alignment is not achieved, it is only a minority that suffer from an axial deviation significant enough to cause visual anomalies (Von Noorden, 1990). This pathological condition is usually referred to as strabismus or squint.

There are two kinds of strabismus: In convergent strabismus, one eye is deviated inwards with respect to the fixation point of the other eye, while in divergent strabismus the visual axis of the misaligned eye is rotated laterally. Different strategies are used by strabismic subjects to circumvent the misalignment problem. The patient uses either an alternating fixation pattern or continuously favours one eye for fixation. In the latter case, the underused eye will irrevocably lose its function unless treated before an average age of seven years (Lithander, 1998) with its maximum of reversibility before three years of age and its minimum from twelve years onwards (Epelbaum et al., 1993). The functional loss of the underused eye is called amblyopia (Von Noorden, 1990). Some studies have claimed that amblyopia is mainly associated with convergent squint (Mitchell et al., 1984; Von Noorden, 1990) whereas others did not find any difference between the two forms of strabismus (Cleland et al., 1982).

Both in convergent and divergent strabismus, the brain is confronted with a perceptual dilemma which can be quite distressing for the individual patient. Due to the misalignment of the optical axes, different objects are either projected onto

corresponding areas of the two retinae (the two foveae) and are therefore perceived as overlapping. Or an identical object is imaged on different parts of the retina (the fovea of one eye and the peripheral retina of the other eye) and is therefore seen twice. The former case is termed confusion, the latter diplopia or double vision (see fig. 5).

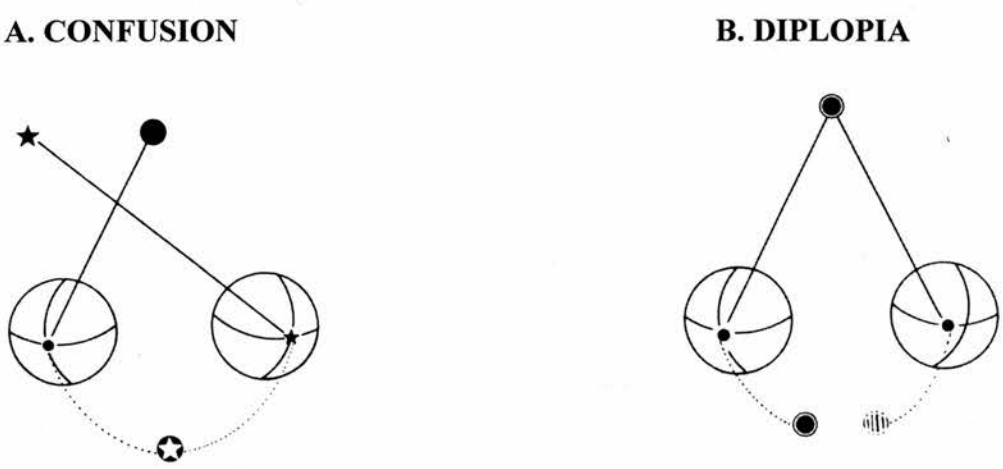

Fig. 5: Effects of the relative deviation of the visual lines. A: Confusion; B: Diplopia (from Von Noorton, 1990, p.201)

To avoid confusion and diplopia, suppression of the incompatible visual information must occur for the deviated eye. Suppression, i.e. temporary functional impairment, and amblyopia, persistent functional impairment, are only encountered in cases of congenital strabismus where complaints of confusion and double vision are relatively rare. In other words, they are neurophysiological strategies of a neuronally immature system to avoid these visual anomalies. In adults on the other hand, acquired strabismus causes constant double vision (Von Noorten, 1990) although true suppression can eventually develop (Wright et al., 1990). What is the neuronal mechanism that underlies amblyopia and suppression?

5.1. Amblyopia

Amblyopia is defined as a "decrease of visual acuity caused by form vision deprivation and/or abnormal binocular interaction for which no organic causes can be detected" (Von Noorton, 1990, p.208).

Only when the dominant eye is covered up, the patient can see with the amblyopic eye. There are a number of characteristic perceptual deficits. Often, the patient is capable of discriminating a small object against a uniform background. If, though, objects are presented in a row, the patient has difficulties in segregating the contours and in avoiding false conjunctions which is attributed to the so-called 'crowding phenomenon' (Levi & Klein, 1985; Rydberg, 1997). Contrast sensitivity can be reduced in the amblyopic eye (Ciuffreda & Fisher, 1987, but see Kiorpes et al., 1998). Other perceptual deficits include temporal instability of the visual picture (Altmann & Singer, 1986) and spatial distortions which are measured in spatial localisation and bisection tasks (Lagreze & Sireteanu, 1992; Sireteanu et al., 1993; Graefe & Haase, 1997).

In the normal striate cortex, many neurons receive input from corresponding points in the two retinae although for most cells the influence is strongest from one eye (Brodal, 1992). However, if squint occurs early in the maturation process of the visual system, the majority of cells in the striate cortex respond to stimulation from one eye only. In other words, binocularity, the ability to integrate information from both eyes is strongly impaired (Von Noorden, 1990).

Imamura et al. (1997) demonstrated decreased cerebral blood flow in the extrastriate visual cortex when neurons driven by the amblyopic eye were stimulated. Interestingly, the number of striate neurons driven by the amblyopic eye is not significantly reduced compared to the one stimulated by the good eye and approximately 10% of all recording sites respond to binocular stimulation (Kalil et al., 1984; Roelfsema et al., 1994). Furthermore, some studies did not find any indication of a reduction in general responsiveness or of a specific reduction of response strength in neurons driven by the amblyopic eye (Eschweiler & Rauschecker, 1993; Roelfsema et al., 1994). On the other hand, Smith et al. (1997) reported decreased response amplitudes in neurons stimulated through the impaired eye. However, a consistently documented abnormality is increased latency of the cortical response to stimulation through the amblyopic eye (Eschweiler & Rauschecker, 1993; Brown & Edwards, 1998; McKerral et al., 1999). Also,

amplitudes of the macropotentials evoked by patterned stimulation of the amblyopic eye appear to be reduced (Yu et al., 1998; Krzystkowa et al., 1998).

Roelfsema et al. (1994) investigated electrophysiological response patterns of the striate cortex in strabismic cats. It was reported that the only pathological findings were impaired synchronised activity between the neurons driven by the amblyopic eye whereas the neurons stimulated by the normal eye showed a significantly stronger synchronisation pattern. Furthermore, synchronised discharge between neurons driven by both eyes was virtually absent. "These results suggest reduced synchronisation of population responses as a neurophysiological correlate of strabismic amblyopia and underline the importance of correlated firing of spatially separate cortical neurons for normal processing of visual information" (Roelfsema et al., 1994). This interpretation would be compatible with the reported decrease of amplitude in pattern evoked potentials (Yu et al., 1998; Krzystkowa et al., 1998) since synchronous discharge is an effective mechanism for amplitude enhancement. Roelfsema et al. (1994, p.1654) claimed further that "reduced synchronisation of responses evoked through the amblyopic eye is likely to reduce the saliency of these responses which would lead to a competitive disadvantage relative to those evoked through the normal eye. This might explain why vision through the amblyopic eye is readily suppressed when both eyes are open".

We will now turn to the suppression mechanism involved in non-amblyopic strabismus and binocular rivalry.

5.2 Visual suppression in non-amblyopic strabismus, binocular rivalry and other examples

In subjects who have developed an alternating fixation pattern, both eyes remain functionally intact but, as in amblyopic strabismus, loss of stereoscopic vision is correlated with a severe reduction of the number of binocular neurons in the striate cortex. Loss of binocularity is a gradual process and, eventually, the vast majority of cortical neurons are exclusively monocular (Chino et al., 1994).

To avoid the visual anomalies of confusion and double-vision, two retinal areas must be suppressed (see fig.5): First, the fovea of the deviated right eye focussing on the

star to avoid confusion. Second, the circle is projected onto the retinal periphery of the right deviated eye. To avoid double vision, this area of the right retina has to be suppressed.

Previous studies have examined the hypothesis that suppression in non-amblyopic strabismus manifests itself by modulation of the firing rate. Thiele et al. (1997) investigated a monkey with late onset strabismus. The results showed that in the striate cortex the neuronal spike response to a stimulus is increased when the eye fixates and decreased when it is not focussing on a fixation point. Sengpiel et al. (1994; Sengpiel & Blakemore, 1994; see also Chino et al., 1994) recorded from the primary visual cortex of cats with surgically induced squint. It was demonstrated that there was a sharp decrease of the monocular neuronal firing rate when a second stimulus was presented to the different eye. This effect was only elicited when the neuron was already responding to a stimulus. No change in firing rate was observed on simultaneous presentation. Furthermore, suppression was independent of the configurational properties of the stimulus (see also Freeman & Jolly, 1994) whereas in normal cats there is neuronal summation after binocular stimulation as long as the stimuli are roughly matched in orientation. Sengpiel and his colleagues (1994; Sengpiel & Blakemore, 1994) proposed inhibitory interactions between neighbouring ocular dominance columns as the cause for suppression.

By contrast, König et al. (1993) examined the temporal correlation of neuronal responses in strabismic cats. As in amblyopic squint, response synchronisation was recorded almost exclusively between cortical cells of the same eye in the striate cortex. However, more interestingly, the few remaining binocular neurons synchronised their activity when activated through one eye but desynchronised when they were stimulated through both eyes. More direct evidence that desynchronisation might be the neuronal substrate for selective suppression comes from a different study that examined non-amblyopic strabismic cats (Fries et al., 1997). Multi-unit recordings of neurons from each eye were performed first under monocular and then after introduction of a rivalrous stimulus. The data showed that monocularly presented stimuli were readily perceived and elicited synchronous discharge in the gamma-band range. However, on binocular stimulation, neurons driven by the

stimulus that continued to be perceived increased synchronicity of the oscillatory discharge whereas the neurons responding to the non-perceived stimulus showed reduced synchronicity. Unlike Sengpiel et al. (1994), Fries and his colleagues (1997) found only a weak correlation between the modulation of discharge rate and the suppression of the rivalrous stimulus. Therefore, Fries et al. (1997) proposed reduced synchronicity as the neuronal substrate for the suppression of incompatible stimuli.

Suppression of rivalrous stimuli is a phenomenon that can also be encountered in normal subjects. The so-called binocular rivalry occurs when two images, each presented to a normal eye, are so dissimilar that they cannot be fused. Typically, the observer describes successive periods of visibility and invisibility of a pattern which are referred to as the eye's 'dominance' and 'suppression' phases. The temporal dynamics of rivalry are influenced strongly by stimulus parameters like luminance, contrast or spatio-temporal frequency (Logothetis, 1998). Whether strabismic suppression and binocular rivalry suppression are based on the same (Sengpiel et al., 1994; Thiele et al., 1997) or different mechanisms (Smith et al., 1985, 1994; Holopigian et al., 1988; de Belsunce & Sireteanu, 1991) is controversial.

Dominance and suppression during binocular rivalry has been thought of as the result of two competing monocular channels in the striate cortex (Blake, 1989). More recently, it has been proposed that binocular suppression/selection occurs at more central levels of the visual system (Leopold & Logothetis, 1996; Sheinberg & Logothetis, 1997; Logothetis et al., 1996; Logothetis, 1998). "It is the 'stimulus' and not the 'eye' that competes for dominance during rivalry". Or in other words, "rivalry may involve competition between alternative perceptual interpretations" (Logothetis et al., 1996, p.624, 621). These claims were based on two findings: Firstly, binocular rivalry can also be elicited by rapidly alternating the rival stimuli between the left and right eye instead of using static patterns (Logothetis et al., 1996). Secondly, discharge patterns of the majority of temporal cortex neurons correlated with the perceptual dominance of an effective visual stimulus (Sheinberg & Logothetis, 1997) whereas only a small percentage of striate, V4 and middle temporal neurons fired

when their preferred stimulus was perceived (Logothetis & Schall, 1989; Leopold & Logothetis, 1996).

Fries et al. (1997) who have proposed modulations of synchronicity in the striate cortex as the neuronal mechanism of suppression or selection during the presentation of two disparate stimuli have pointed out that their findings are reconcilable with the data gathered by Logothetis and his colleagues (Leopold & Logothetis, 1996; Sheinberg & Logothetis, 1997; Logothetis et al., 1996; Logothetis, 1998). Fries et al. (1997) argued that changes in synchronicity at early stages of processing are likely to result in changes of discharge rate at more central levels. "Thus, the rate changes observed with perceptual rivalry ... in higher cortical areas could be secondary to modifications of neuronal synchronization at lower levels of processing" (Fries et al., 1997, p.12704).

Support for this interpretation was provided by a simulation study (Lumer, 1998). Lumer (1998) modelled the mammalian early visual system by using a neural network and discovered specific effects of spike timing on competition. Congruent stimulation of both eyes caused synchronised discharge among binocular neurons in V1. On the other hand, two different stimuli presented to the two eyes resulted in neuronal asynchrony which produced rivalrous response suppression at later stages of the visual system. "The results suggest that input-related differences in relative spike timing at an early stage of visual processing may play an important part in the phenomena both of binocular integration and rivalry; furthermore, they indicate that the temporal patterning of cortical activity may be a fundamental mechanism of selection among competing stimulus presentations" (Lumer, 1998, p.553).

It has been suggested that visual suppression has evolved as a general mechanism to eliminate "stimuli which would otherwise interrupt or destabilize perception" ... "and that might lead to maladaptive responses" (Volkmann, 1986, p.1413).

There are further examples of suppression when visual information from both eyes is incompatible. Richards (1968) reported elevations in threshold, albeit small ones, after passive movements of the eye by tapping the eye ball - a manipulation which also produces double vision by bringing the eyes' axes out of line. Furthermore, visual sensitivity is reduced during saccades although not completely abolished

(Bridgman & Fisher, 1990; Bridgman & Macknik, 1995; Uchikawa & Sato, 1995). This phenomenon is usually referred to as saccadic suppression (Zuber & Stark, 1966; Volkmann, 1986). Consequently, the intake of visual information from the environment is mainly restricted to fixations. Uptake of visual data has to be distinguished from cognitive processing. There is an ongoing debate as to the extent of suspension of cognition during saccades (for a review see Irwin, 1997). Interestingly, considerable transient disparities between the two optical axes have been documented during saccades. The disparity arises because, in a typical horizontal saccade, the abducting eye accelerates more quickly than the adducting eye, i.e. the abducting eye reaches the target more quickly (Collewijn et al., 1988, 1997). Retinal mechanisms as the source of suppression have been considered less likely because elevated thresholds are measured *before* the onset of a saccade. The maximum of suppression is reached during the saccade and it gradually disappears over several tens of milliseconds after the saccade has been completed (Zuber & Stark, 1966; Volkmann, 1986). Therefore, one might hypothesise that saccadic suppression is a programme that is activated centrally to protect the visual system from disparate information.

To summarise, visual suppression might be regarded as a mechanism by which the visual system selects information. Examples from amblyopia, strabismus and binocular rivalry have illustrated how reduced synchronicity might be correlated with the impaired perception and suppression of visual stimuli. The nature of suppression in amblyopia can be both passive, due to 'reduction of saliency leading to a competitive disadvantage' (Roelfsema et al., 1994), and active through the neurons driven by the intact eye. On the other hand, suppression in non-amblyopic strabismus, binocular rivalry and during saccadic eye movements appears to be mediated by excitatory processes to increase inhibition of the incompatible or rivalrous stimuli.

We will now present a framework of unilateral neglect which is based on this principle of disrupted synchronised neuronal activity.

6. Unilateral neglect as temporal diplopia

We will first summarise the evidence discussed so far that has led to the development of the ideas presented in this study:

- Imaging and electrophysiological studies have provided evidence for a general slowing down of neuronal activity after stroke which affects mainly the damaged hemisphere but can involve the 'healthy' hemisphere.

- Synchronous activity in the central nervous system is a widespread phenomenon. There is mounting support for its role in perceptual and cognitive processes.

- Disruption of synchronicity might lead to perceptual impairment as the examples of strabismus and binocular rivalry have illustrated.

We will now continue by presenting evidence for changes in the temporal dynamics of information processing which affect both stroke patients with and without unilateral neglect. We are examining evidence that processing in the affected hemisphere is more slowed down than in the unaffected hemisphere.

6.1. Temporal abnormalities of information processing in unilateral stroke patients

Rorden et al. (1997) examined two patients suffering from visual extinction after unilateral right parietal damage. Stroke patients without extinction or neglect were not included in the paradigm of temporal order judgement. The control group consisted of two normal subjects. Extinction has been regarded as a related but nevertheless minor form of unilateral neglect (Critchley, 1950; Denny-Brown et al., 1952; Mesulam, 1981; Posner et al., 1984; Riddoch & Humphreys, 1987; Bisiach & Berti, 1987; Karnath, 1988; Bisiach, 1991; Heilman et al., 1993).

The patient was sitting in front of a computer screen on which first a central cross appeared. This cross remained in place for the duration of the trial to provide a continuous central fixation point. Then a short horizontal line appeared on the left side, the side of extinction, followed by a second short horizontal line on the right

side. The task of the patient was to indicate on which side the line first appeared. The results showed that the line on the left had to precede the one on the right by 200 ms to be perceived as appearing first. The authors interpreted the results as a prior-entry phenomenon. Titchener (1908) postulated in his prior-entry law that "the stimulus for which we are predisposed requires less time than a like stimulus, for which we are unprepared, to produce its full conscious effect" (quoted by Rorden et al., 1997, p.422). Rorden et al. (1997) rephrased the concept of prior-entry by stating that "an attended stimulus will be experienced sooner than a physically simultaneous unattended stimulus". Applying the principles of temporal correlation theory and the claim of neuronal slowing down after stroke, prior entry might also imply that an object processed by normal neurons is perceived before a second object which is processed by impaired and slowly functioning neurons. In other words, awareness and attention are defined as a function of the speed and synchronicity of neuronal processing.

Similar results were reported by Birch et al. (1967) who examined a group of 24 right hemisphere damaged patients for tactile extinction. In 19 patients the performance did not reached 100% on simultaneous stimulation of both forearms with seven patients responding correctly above chance levels but not reaching maximum scores. All 19 patients improved when the stimulus presented to the contralesional arm preceded the one applied to the ipsilesional arm. Birch et al. (1967) concluded that extinction was caused by slowed afferent processing in the damaged hemisphere. It should be stressed here that even patients who showed extinction responses in only a few trials benefited from changing the temporal pattern of stimulus presentation (see also Swisher & Hirsh, 1972, for the auditory modality).

Duncan (1998) demonstrated that deficits in extinction patients do not arise on simultaneous presentation of rivalrous stimuli only. Arrays of five letters were presented to the extinction patient either in the left or the right visual fields but not bilaterally. The stimuli were flashed onto the screen for different durations which lasted for up to 400 ms. The results showed that the number of letters reported increased exponentially with increase in exposure duration. However, the increase was significantly slower in the extinction patient than in the control patient.

Furthermore, the processing rate of the extinction patient was slower in the contralesional visual field compared to the ipsilesional hemifield.

Rorden et al. (1997) suggested that the auditory localisation paradigm might be another example for prior entry phenomena. For example, Bisiach et al.(1984) studied unilateral hemisphere patients and divided them into four groups: Left hemisphere patients with visual field loss, left hemisphere patients without visual field loss, right hemisphere patients without visual field loss and right hemisphere patients with field loss. The last group was further subdivided in patients who displayed symptoms of visual neglect in a line cancellation task and patients who did not. The patients were tested in a dichotic listening paradigm. Pure tones were presented to both ears and lateralisation was achieved by adjusting intensity differences as opposed to interaural time differences (see for example Walsh, 1957). The subjects were asked to report their perceptions of location of the acoustic image by pointing with their forefinger to the skull in the coronal plane passing though the ears. Lateralisation normally occurs towards the side which received the more intense stimulus. The following results were reported: Whereas the patients with right and left hemisphere damage without any visual field loss performed at the same level as the normal controls, right hemisphere damage patients with visual field loss displayed a significant impairment in the localisation task. These patients displaced the sound towards the side ipsilateral to the damaged hemisphere. Interestingly, unilateral neglect patients with visual field defects displayed a higher mean standard error than right hemisphere patients with field defects but *without* neglect symptoms. However, the difference was not significant.

The association of visual field loss and impaired localisation performance is not immediately obvious. Bisiach et al. (1984) mentioned that the size of the lesion is more severe in patients with neglect but do not address how big the lesions are in patients without visual field loss. It can only be suggested that in patients with visual field loss the extent of the damage is more severe usually involving the blockage of the middle cerebral artery which supplies the visual projections from the lateral geniculate corpus to the occipital cortex. Therefore, functional impairment would be more significant and more easily detectable in the auditory localisation task.

However, there is no immediate explanation why patients with visual field loss and left hemisphere damage perform well, as the site and extent of the lesions were comparable to the group with visual field loss and right-sided damage.

Abnormal temporal dynamics in the processing of visual information in neglect patients was reported by Husain et al. (1997). The data revealed a three-fold increase of the so-called attentional blink in unilateral neglect patients compared to the control group. The attentional blink is defined as the time during which attention cannot be allocated to a novel stimulus after attention has been focussed on a object. Unfortunately, the issue of hemispace effects was not addressed in this study and the stimuli were only presented in central location. Furthermore, the stroke patients without neglect in the control group had attentional blink times as short as healthy control subjects. However, the absence of increased attentional blink times in non-neglect stroke patients could be explained by the fact that a potential increase in the contralesional hemispace was too small to have an effect when the stimulus was presented centrally.

Electrophysiological studies provide more direct evidence for the speed of neuronal processing. The electrophysiological changes that are of importance in this context are, first, the lengthening of latencies in visual evoked potentials (VEPs) and, second, slow wave neuronal activity in EEGs which emerge mainly in the damaged hemisphere. Decreased amplitudes of electrical signals could also be interpreted as indirect evidence for disrupted temporal dynamics. However, amplitude changes could also be observed in a neural system where a rate code is used and temporal information is completely irrelevant.

Lhermitte et al. (1985) recorded event-related potentials in a group of nine neglect patients in an attentional task where stimuli were presented either to the left or right visual field. Their data showed an increased latency and decreased amplitude of wave P 300. This result was specifically related to neglect patients and did not occur in non-neglect stroke patients and normal subjects. Wave P 300 is associated with stimulus evaluation and stimulus categorisation. By contrast, early components of

sensory processing were normal in the neglect group. Furthermore, no significant wave P 300 differences were discovered when the event-related potentials in the auditory modality were examined.

Spinelli et al. (1994) recorded steady-state visual evoked potential in a group of neglect subjects, non-neglect stroke patients and normal controls and demonstrated that early visual processing can be affected in unilateral neglect. VEPs from the contralesional hemifield were delayed by 30 to 40 ms in neglect patients whereas there was no change in amplitude of the VEPs. These results were confirmed by Angelelli et al. (1996) who used the same paradigm. Spinelli et al. (1996) suggested that the delay observed in neglect patients might be due to a selective damage to the magnocellular system which has short latencies to visual stimulation whereas the parvocellular pathway has long ones. The latter system projects mainly to anterior temporal cortical areas whereas the former sends its projections to the dorso-lateral posterior parietal areas. This suggestion was confirmed in a study involving ten neglect patients where the magnocellular and parvocellular systems were selectively stimulated with either different or same luminance stimuli. VEP latencies were only reported after contralesional presentation of stimuli that activate the magnocellular system. However, an alternative interpretation would be that dissociations of latencies to different stimuli might emerge depending on which areas are involved in the structural and functional impairment following cerebral trauma and that the observed dissociation (Spinelli et al., 1996) is not at all specific for neglect patients. This view is supported by a study of Doricchi et al. (1996). In a single case study involving a left neglect patient who had suffered a massive stroke, increased latencies were also demonstrated from the contralesional visual field after the presentation of stimuli which activated the parvocellular system.

Pitzalis et al. (1997) provided evidence for delayed processing not only in the horizontal but also vertical dimension of neglect patients. Steady-state VEPs were measured in all four quadrants of the visual field. In neglect patients with right hemisphere damage who displayed most omissions in the left lower field, VEPs recorded from the left lower quadrant had the longest latencies. This result was a reversal of the data obtained from normal control subjects whose VEPs from the left lower quadrant displayed the *shortest* latencies.

Not every study reported changed temporal dynamics after cerebral damage. Vallar et al. (1991) examined a small group of neglect patients and did not discover any abnormalities in both VEPs and somato-sensory evoked potentials. Similarly, Verleger et al. (1996) investigated VEPs in a group of right hemisphere patients which displayed various degrees of unilateral neglect. No change in the temporal pattern of the VEPs was discovered. However, Spinelli et al. (1994) pointed out that the failure to demonstrate any latencies in Vallar et al.'s study (1991) might be due to the fact that transient VEPs were recorded as opposed to steady-state VEPs which appear to be more sensitive.

So far no evidence for slowing down of neuronal processing in non-neglect stroke patients has been provided by evoked potential studies. However, Viggiano et al. (1995) tested steady-state VEPs of ten neglect, eleven unilaterally brain damaged patients without neglect and normal controls. No abnormalities of the VEPs were reported when they were presented in the ipsi- or contralesional visual field. If the stimulus was projected on a central fixation point, though, unusual response patterns emerged both in the neglect and non-neglect patients group. The stimulus was circular and subtended 15 degrees of visual angle. Therefore, if in a central position it extended well into the left and right visual fields. Normally, when a stimulus is presented simultaneously in both visual fields, there is a summation effect in that the response amplitude equals the sum of the amplitudes of each separate visual field. Spinelli et al. (1994) had previously reported that in neglect patients the response to bilateral stimulation was similar in amplitude to the response of either hemisphere alone. "This probably results from the fact that the two hemispheres are out-of-phase" (Spinelli et al., 1994, p.915). The same phenomenon was observed by Viggiano et al. (1995) but it affected not only the neglect but also the left and right non-neglect patients. Interestingly, the degree of summation loss was graded. Normal controls had the highest summation amplitudes. Neglect patient did not have any summation at all, whereas the left and right non-neglect group showed some summation but clearly much less than normal subjects. This result could be interpreted as evidence for the claim that even in non-neglect patients the two hemispheres are operating slightly out of synch. Decreased summation of VEP

amplitude might be a more sensitive measure for temporal changes than detecting a latency increase in unilateral VEPs.

Watson et al. (1977) provided further support for the claim that slowing down is present in neglect and non-neglect patients but that the degree of slowing is less pronounced in the latter group. EEG abnormalities were documented in a group of 23 neglect patients and 21 matched non-neglect unilaterally damaged subjects. In the neglect group, EEGs in 22 patients showed slowing in the theta and delta band that extended over the entire damaged hemisphere and focal slowing restricted to the parieto-temporal region of one patient. In the non-neglect group, eight out of 20 patients had EEG slowing over the entire hemisphere. The incidence of diffuse slowing in the EEG traces was significantly higher in the neglect group. Demeurisse et al. (1998) who examined a group of patients following right-sided subcortical strokes reported similar findings. Sixteen patients did not display signs of neglect whereas 17 patients were assigned to the unilateral neglect group. However, the main result was a reduced left-to-right ratio of slow delta activity between posterior homologous regions in the neglect group.

The above review has illustrated that slowing down of neuronal processing occurs in both neglect/extinction patients and in stroke patients who do not show symptoms of unilateral neglect. In the next section, we will present our own approach to unilateral neglect.

6.2. **The temporal diplopia theory**

Based on what has been discussed so far in this chapter, we claim the following:

Claim 1: Impaired synchronised neuronal activity *within* the damaged hemisphere and *between* the two hemispheres is the underlying neurophysiological mechanism of many symptoms observed in unilateral neglect patients.

Claim 2: The consequence of impaired intrahemispheric synchronisation is:

- Representations in the damaged hemisphere lose saliency due to a weakening of the electrophysiological signal. The binding and integration of information within the damaged hemisphere are impaired.

The consequence of impaired interhemispheric synchronisation is:

- The damaged hemisphere is out of phase with the undamaged hemisphere due to unilateral slowing down. The binding and integration of information between the hemispheres are impaired.

- The brain is faced with a processing dilemma of incompatible information: "Temporal double vision". The problem extends to both the sensori-motor system and cognitive processes.

Conscious perception of some part of the contralesional world is not experienced. This unilateral loss of consciousness is mediated by a combination of active and passive mechanisms. There is active suppression of the damaged hemisphere by the intact hemisphere. Other examples of suppression of incompatible information are found in amblyopia, binocular rivalry and saccadic suppression. A passive mechanism for losing conscious representation of the neglected information is the diminished neuronal signal in the damaged hemisphere.

Claim 3: Unilateral neglect, therefore, does not exist as a neuropsychological entity. It is the product of a disrupted basic processing mechanism and the extreme manifestation on the spectrum of unspecific unilateral cerebral damage. Consequently, similar, but attenuated, patterns of impaired processing should emerge in stroke patients without neglect.

6.2.1. Explanatory power of the theory

In this section we will discuss our claims in connection with symptoms that extend Heilman's taxonomy of unilateral neglect (Heilman, 1993). However, the symptom of anosognosia is not addressed because of recent evidence that it is not associated with unilateral neglect (Stone et al., 1998).

6.2.1.1. Contralesional and ipsilesional neglect

One of the least disputed characteristics of neglect is the fact that the space contralateral to the lesion is affected. Since the organisational principles of the motor and somato-sensory system in the human central nervous system is the contralateral projection of the neuronal pathways (Brodal, 1992), our theory can easily accommodate the spatial distributions of neglect symptoms.

Furthermore, in some cases neglect has not been strictly been confined to the contralesional hemispace (e.g. Apfeldorf, 1962; Small et al., 1994). We have illustrated above that the non-affected hemisphere might also be involved in the pathological changes following cerebral damage (Celesia et al., 1984; Fiorelli et al., 1991; Perani et al., 1993). Therefore, our theory can account for ipsilesional neglect by claiming that focal slowing down and desynchronisation of neuronal activity in the 'intact' hemisphere can lead to neglect of stimuli or parts of stimuli in the ipsilesional hemifield.

6.2.1.2. Unilateral neglect more frequent and severe after right hemisphere damage

Impaired synchronisation due to cerebral damage is a mechanism that is not specific to one side of the brain. Therefore, increased frequency and severity of unilateral neglect after right hemisphere damage (Brain, 1941; Critchley, 1950; McFie & Zangwill, 1960; Arrigoni & De Renzi, 1964; Benton, 1969; Faglioni et al., 1971; Gainotti & Tiacci, 1971; Gainotti et al., 1972; Chedru, 1976; Schenkenberg et al., 1980; Mesulam, 1981; Denes et al., 1982; Kinsbourne, 1987; Massironi et al., 1988; Heilman et al., 1993; Spiers et al., 1993) should be a consequence of differences in neuroanatomical properties and processing strategies between the different hemispheres.

It has been proposed that the principle of coarse coding is more developed in the right hemisphere compared to the left hemisphere (Kosslyn et al., 1992; Beeman, 1998). "Coarse coding is representation by a small number of variables used in combination, rather than by a large number of variables most of which will be zero on any particular occasion" (Barlow, 1995, p.423). The neuroanatomical substrate of coarse coding is large overlapping receptive fields. The representation by each receptive field is inexact, i.e. coarse, but a system of overlapping representations can produce precise information. Consequently, if one were to claim a correlation between coarse coding and the right hemisphere, there should be more connectivity on the right side compared to the left hemisphere as each cell or neuron population at one level is connected to a relatively larger number at the next level.

Beeman (1998) reviewed the neuroanatomical evidence for this prediction. For example, Gur et al. (1980) demonstrated that there is a higher ratio of white to gray matter in the right hemisphere. Furthermore, evoked potentials over the right hemisphere appear more diffuse than those recorded over the left side (Trotman & Hammond, 1989) and greater EEG coherence was documented over the right than the left hemisphere (Tucker et al., 1986).

Coarse coding has implications for synchronisation: The coarser the coding, the larger the receptive fields. The larger the receptive fields, the longer the distances that cortico-cortical association fibres have to travel between levels. This organisational principle is therefore more vulnerable to disruptions of synchronised discharge than a neuronal system with small receptive fields which could explain why unilateral neglect is more frequent, severe and/or long-lasting after right hemisphere damage.

From this it could further be claimed that right hemisphere patients without any signs of neglect or extinction are more likely to present with impaired processing than left hemisphere patients. For example, Smania et al. (1998) studied the visual field distribution of speed and accuracy of manual responses to small brief light flashes. The test groups included left and right hemisphere patients with and without extinction or neglect symptoms. The results demonstrated that the right hemisphere group without neglect or extinction performed significantly worse than the left hemisphere group without neglect or extinction.

6.2.1.3. Motor neglect and directional hypokinesia

Since we are postulating the disruption of a basic processing mechanism, desynchronisation of neuronal discharge could occur at any level depending on regional metabolic and blood flow conditions.

Motor neglect has been defined as the under-utilisation of the contralesional limb (Laplane & Degos, 1983; Bisiach et al., 1990). The functional impairment causing motor neglect could affect any process that is involved in the planning and execution of a motor task. For example, the underused limb might not be integrated in the generation of motor programs because there is no conscious perception of the limb due to desynchronisation of the proprioceptive input. Alternatively, normal neuronal processing in the anatomical centre could be compromised which normally integrates sensory information to direct and plan spatial movement, like for example the inferior parietal cortex (Mattingley et al., 1998).

Directional hypokinesia is referred to as the reluctance or the failure "to initiate or carry out motor activities toward the contralesional side of egocentric space, irrespective of the side of limbs involved in such activities" (Bisiach et al., 1990, p.1278). Mattingley et al. (1998b) examined the effects of target predictability and motor reprogramming on visuomotor selection in right hemisphere patients with and without left neglect. It was predicted that neglect patients have a bias to select responses towards ipsilesional targets. The time was measured that was required to execute movements to an occasional, unpredictable target occurring during a sequence of well-trained, reciprocating movements between horizontally adjacent buttons. The task was performed with the right hand. All three groups performed equally well when executing predictable and reciprocating movements. However, as soon as unpredicted targets were presented an interesting pattern emerged. The data showed that neglect patients were slower to reprogram unexpected contralesional movements compared to movements into the ipsilesional direction. Furthermore, the same effect was also found in the right hemisphere group without neglect although the difference was only slight. "These findings suggest that the competitive bias favouring movements towards ipsilesional targets may also occur in milder form among patients who do not show signs of neglect on standard clinical tests" (Mattingley et al., 1998b, p.253). As the underlying mechanism for this competitive

bias Mattingley et al. (1998b) proposed that responses towards ipsilesional stimuli are triggered more quickly than motor programs towards stimuli in the contralesional direction.

These findings are very much compatible with our theory: First, competitive disadvantages arise due to decreased speed in the processing of the damaged hemisphere. Second, the effects are also found in non-neglect stroke patients but in an attenuated form.

6.2.1.4. Dissociations and fluctuation of performance

The fact that desynchronisation can emerge focally might explain the various dissociations that have been documented in unilateral neglect (e.g. Bellas et al., 1988; De Renzi et al., 1989 b; Guariglia et al., 1993). Depending on which area of the brain is out of synch with the rest of brain, neglect will affect some modalities or reference frames and not others.

Furthermore, neglect patients tend to display a surprising degree of fluctuation in their clinical symptoms. Sometimes, the level of performance can vary even from one moment to the next (but see Levy et al., 1995). In patients whose neglect symptoms have a vascular origin the answer to these fluctuations might lie in the neurophysiology of a diseased cardio-vascular system and the changes after stroke. In a healthy subject, the cerebral blood flow is held constant over a wide range of cerebral perfusion pressures. The cerebral arteries constrict as the systemic arterial pressure rises and dilate as it decreases. This phenomenon is called autoregulation and is effective between mean arterial pressures of 60 to 130 mmHg. Below and above these limits, the cerebral blood flow changes passively with the perfusion pressure, i.e. it is dependent on how much the heart is pumping to the brain. Many patients who have suffered a stroke have had a past medical history of hypertension. In hypertensive patients the boundaries of autoregulation are moved up, e.g. to 90 and 160 mmHg (Aitkenhead & Smith, 1990). In situations of blood pressure below 90 mmHg, the brain is then directly dependent on the cardiac output. As we have seen, after stroke there is widespread hypoperfusion both in the infarcted and the intact hemisphere which means that the perfusion pressures are low. If the blood pressure drops below the critical lower boundary below which autoregulation ceases

to be effective, the brain is at risk of suffering from lack of oxygen (Skyhøj Olsen et al., 1986). In other words, the performance of a neglect patient might be influenced by the consumption of a cup of coffee which increases cardiac output. Similarly, if a patient has just woken up from a daytime nap, cardiac output and cerebral perfusion might drop below the critical cut-off line. Depending on the degree of malperfusion, desynchronisation will be ameliorated or accentuated as a function of cardiac output which is correlated with an improvement or worsening of the neglect symptoms, respectively.

6.2.1.5. Implicit processing, allochiria and some therapeutic implications

Several reports have illustrated that although the neglect patient denies conscious awareness of neglected stimuli, the processing of the stimuli interferes with the patient's actions and responses (Marshall and Halligan, 1988; Bisiach and Rusconi, 1990; Young et al., 1992; Làdavas et al., 1993; Mijovic-Prelec et al., 1994; but see Behrmann & Megan, 1998).

Allochiria is different in that not all stimuli located in the contralesional hemispace are neglected. In this case, target stimuli are displaced towards the ipsilesional hemispace (Halligan et al., 1992; Guariglia et al., 1993). We agree with Audet and colleagues (1991): "It seems that the nature of processing in the neglected field may be dependent on the severity of the disorder" (Audet et al., 1991, p.21). We hypothesise that in allochiria the extent of interhemispheric desynchronisation is not as severe as in cases where no conscious processing occurs. Allochiria could be defined as a perceptual compromise: Instead of losing the images of temporal double vision altogether, parts of it are transposed onto the ipsilesional side.

It is predicted that if fewer or no rivalrous representations are generated in the intact hemisphere, processing in the damaged hemisphere should improve except for cases where the tissue damage is extensive.

Mark et al. (1988) demonstrated that the performance of neglect patients improved in a line cancellation task when the lines were cancelled by removal instead of being marked by the patient which "suggests that hemispatial neglect is influenced by the presence of stimuli in the non-neglected hemispace" (Mark et al., 1988). Hjaltson

and Tegnér (1992) modified a standard line bisection task by using a luminous line which consisted of LEDs. There were two conditions: Normal illumination and darkness. Left neglect patients made large rightward errors under normal illumination as it was expected but the rightward deviation decreased in darkness by 43%. Hjaltson and Tegnér (1992) proposed that the improvement might be due to the elimination of extraneous visual stimuli from the ipsilesional hemispace. Similarly, Halligan and Marshall (1994b) reported a single case study of a severe left neglect patients who when asked to draw a butterfly with the eyes open omitted the left side of the object. When asked to do the same with eyes closed, a full butterfly was produced. Chedru (1976) examined left and right hemisphere patients with and without neglect. The subjects were required to tap the keys all over a teletype keyboard. The task was first performed with a blindfold and then with open eyes. There was improvement in the blindfold condition. However, it is not clear why only the hemianopic neglect patients performed better in the blindfold condition whereas neglect patients without a visual field defect deteriorated.

Beis et al. (1999) investigated two different rehabilitation techniques that have been used with unilateral neglect patients. In one case, the ipsilesional eye of the neglect patients was patched up. In the other only the retinal areas that receive input from the non-neglected visual hemifields were covered up. The rationale for ipsilesional monocular patching was based on the observation that in primates the superior colliculus receives most of its input from the contralateral eye (Hubel et al., 1975). The superior colliculus is a structure known to be activated in the programming of saccadic eye movements. It was further proposed that by patching the ipsilesional eye of neglect patients the input to the contralesional superior colliculus which is involved in the programming of rightward saccadic movements would be reduced. In this way, the bias to direct eye movements to the ipsilesional space would be decreased. By contrast, blocking the input from the intact ipsilesional hemifields would stimulate the damaged hemisphere in isolation. Beis et al. (1999) split the neglect patients into three groups: One group did not receive any treatment, one group received a complete eye patch for the ipsilesional eye and the last group was given half-eye patches to cover up the ipsilesional hemifields. After three months, during which time the two groups wore the patches for twelve hours daily, the

following differences emerged: There was a significant improvement between the control group of neglect patients and the subjects that wore the half-patches whereas there was no significant difference between the monocular patch group and the neglect control group (but see Butter & Kirsch, 1992, where eleven of 13 neglect patients improved in at least one out of five neglect tests after monocular patching). The improved performance scores also became obvious in activities of daily living.
Arai et al. (1997) only employed the half-patch technique in their study. The results were not as clear-cut: Out of ten left neglect patients, four subjects improved their performance in a line bisection task, four did not change and two deteriorated. In a line cancellation task, three patients improved and seven did not change their results. Finally, four patients improved their performance in a figure copying task whereas the results stayed the same for six subjects. However, the patching of the ipsilesional hemifields had dramatic effects on one patient. At eight months post-onset of the neglect, the patient repeatedly walked into objects on his left side. When given the hemispatial sunglasses that filtered 70% of light on its passage to the intact hemifield, the patient's performance improved immediately. He wore the glasses for an entire week and stopped colliding with objects. The effect continued for beyond that week although the patient was no longer wearing the glasses. Unfortunately, Arai et al. (1997) did not specify when the patient stopped showing improved performance.

These examples have illustrated that the removal of rivalrous representations generated through the intact hemisphere can lead to significant changes in the performance of neglect patients. The treatment of strabismus by patching both eyes alternately (Von Norden, 1990) or constraint-induced movement therapy in patients with chronic motor deficits (Miltner et al., 1999b) could be interpreted as instances of a similar approach. In the latter case, the motor impairment of chronic stroke patients was treated by restricting the movement of the intact upper extremity by placing it in a sling for 90% of the day for twelve days. During that period, the affected extremity was trained for seven hours daily on eight weekdays. The results showed a marked improvement in the motor activities of the impaired extremity after treatment (Miltner et al., 1999b).

6.2.1.6. Temporary remission of unilateral neglect and cueing

If, as postulated, the two hemispheres are desynchronised, there should be two possibilities of boosting the performance of the damaged side: Either, as described above, the activity of the intact hemisphere is reduced, or alternatively, the neuronal processing of the damaged one is speeded up.

Temporary remission of neglect has been described after contralesional optokinetic stimulation (Pizzamiglio et al., 1990), transcutaneous electrical stimulation of the contralesional neck muscles (Karnath et al., 1993; Vallar et al., 1995) or caloric testing (Rubens, 1985). What are the electrophysiological correlates of this kind of stimulation?

Spinelli and Di Russo (1996) recorded steady-state visual evoked potentials (VEPs) in four patients with left unilateral neglect after stimulating either the left or the right visual hemifield. In the standard condition, when body and head were aligned and oriented straight ahead towards the stimulus, the VEPs from the left visual hemifield were delayed compared to stimulation of the right hemifield. However, when the body was turned to the left with the head remaining in the standard position, there was no VEP latency difference between the hemifields. In other words, sensory extra-retinal afferents from the left stretched neck muscles decreased VEP latencies and restored the altered cerebral activity.

A different example of accelerated neuronal processing after stimulation was presented in a single case study by Storrie-Baker et al. (1997). Neglect symptoms and EEG patterns were recorded in a left neglect patient before and after the irrigation of the left external ear canal with iced water. After caloric stimulation, there was a temporary partial remission of the neglect symptoms which was accompanied by significant changes in the EEG. There was a general increase of fast-wave activity and a reduction of slow-wave bands. The effect was observed over both hemispheres but was significantly more pronounced over the right side.

Cueing is another example of the stimulation of the damaged hemisphere. The effects of cueing in connection with unilateral neglect have been the object of controversy (Heilman & Valenstein, 1979; Riddoch & Humphreys, 1983; Halligan & Marshall, 1989b). Different forms of cueing have been used ranging for example from sensory

stimulation (Mattingley et al.,1994), spatio-motor cueing (Halligan et al., 1991), lexical cueing (Brunn and Farah, 1991) to 'internal' cueing (Bisiach et al., 1981).
We hypothesise that the stimulation and activation of different cueing techniques might have the same effect as the ones described above: Namely, the acceleration of neuronal functioning in the damaged hemisphere. However, whether the patients respond to cueing might depend on the severity of the cerebral destruction as opposed to the degree of functional impairment.

6.2.1.7. Hyperattention and attentional gradients

Kinsbourne (1987, 1993) introduced the concept of the attentional gradient. It was suggested that each hemisphere acts as an opponent processor with its own attentional gradient. The attentional bias created by the left hemisphere was assumed to be stronger than the one of the right hemisphere. Kinsbourne's claims, therefore, predict a paradoxical increase of attention from the centre to the periphery in the ipsilesional hemifield after unilateral damage which is usually referred to as 'hyperattention'.
De Renzi et al. (1989) presented letters in four positions in the ipsilesional hemifield. In a search task, right hemisphere patients with and without neglect were asked to respond to the target letter. The data showed that the left neglect patients' reaction times became progressively faster as the target position moved to the periphery of the ispilesional hemispace. In contrast, the position of the target letter had no effect on the reaction times of the right hemisphere group without neglect.
Comparable results were reported by Làdavas et al. (1990). In a similar experimental paradigm, right hemisphere patients with neglect reacted faster to right-relative positions of the target stimulus. In fact, the response times to the right-relative target were even faster than the ones produced by the right hemisphere patients without neglect. In the study by Làdavas et al. (1990) only the central 15 degrees of the visual field were explored.
Smania et al. (1998) did not only extend the range of exploration within one visual field to 40 degrees along the horizontal meridian but also included the contralesional hemispace. Four groups were examined in an experiment that tested the visual field distribution of speed and accuracy of manual responses to short light flashes: Left

neglect patients, left extinction patients, left and right hemisphere patients without neglect or extinction and normals. Detection accuracy of the stimulus in neglect patients demonstrated the same paradoxical effect that De Renzi et al. (1989) and Làdavas et al. (1990) had reported: The more right the position, the more accurate the response. This observation applied to both the left and the right hemifields. In contrast, the position of the target in the ipsilesional field did not influence the accuracy of the remaining groups. Smania et al. (1998) interpreted the data as evidence in favour of Kinsbourne's attentional gradient theory (1987, 1993).

Andersen et al. (1990) provided neuroanatomical evidence for an attentional gradient. The study investigated the receptive field distribution in the parietal cortices of macaque monkeys. The results demonstrated that although most neurons of area 7a had large bilateral receptive fields, the centres of the receptive fields (the retinal location at which maximum responses are recorded) are located in the contralateral visual field (for a neural network model of the attentional gradient see Pouget & Sejnowski, 1995, 1996).

Rizzolatti et al. (1985) developed a model of how the receptive field distribution of neurons in the post-arcuate cortex of the monkey might lead to an 'attentional' gradient. The proposals were later extended to humans by Bisiach and Vallar (1988). Rizzolatti et al. (1981) had found that 29% of neurons had exclusively contralateral receptive fields, 3% exclusively ipsilateral and 68% had bilateral receptive fields. Furthermore, bilateral receptive fields extended horizontally from the midline to a variable extent. It was concluded that the extreme periphery of each hemispace is represented exclusively contralaterally whereas, as one approaches the centre, the representation becomes increasingly bilateral. Consequently, a unilateral lesion will affect the left and the right hemifields. The attentional gradient will have its minimum strength in the extreme contralesional and its maximum strength in the extreme ipsilesional hemifield.

The model of desynchronisation can make specific predictions on attentional gradients only for cortical areas that are topographically organised: In the striate cortex the projections between a neuron representing an area in the periphery of the left visual field and the cortical area representing the centre of the left visual field are

longer than the projections between two central points in the left visual field. Thus, after cerebral damage, an attentional gradient within the visual field with the maximum at the periphery and the minimum in the centre emerges if we adopt Singer's claim (1998) that attention and binding are mediated by synchronised discharge between neuronal populations. However, this line of reasoning does not apply to homotopic striate cortical areas *between* the two hemispheres as the more central areas of the visual field are represented more posteriorly than the peripheral ones, i.e. interhemispheric connections are longer between corresponding central areas than peripheral areas (Brodal, 1992; for a review of the cortico-cortical connectivity in the visual system see Kennedy et al., 1991). As for the somato-sensory and motor cortical systems, it is hypothesised that the contralesional face and the arm are more affected by neglect as the somatotopic representations of the leg and foot are closer to the cerebral sagittal plane. To our knowledge, there are no studies that have examined this specific aspect of neglect symptoms, yet.
Finally, it has to be pointed out that the parietal cortices which are frequently associated with unilateral neglect (Vallar, 1993) have the longest homotopic cortico-cortical association fibres.

6.2.1.8. Extinction

Sensory extinction may be defined as the failure to perceive and to respond to one of two simultaneously applied stimuli although each stimulus is detected correctly when presented on its own. Usually, the extinguished stimulus refers to the stimulus that has been presented to the side contralateral to the lesion.

Several studies have reported a double dissociation between the extinction and neglect phenomena (e.g. De Renzi et al., 1984; Posner et al., 1984). Therefore, the question whether extinction and visuo-spatial neglect are related disorders (e.g. Critchley, 1950; Denny-Brown et al., 1952; Friedland & Weinstein, 1977; Mesulam, 1981; Posner et al., 1984; Riddoch & Humphreys, 1987; Bisiach & Berti, 1987; Karnath, 1988; Bisiach, 1991; Heilman et al., 1993) or whether extinction should be regarded as an independent phenomenon (e.g. De Renzi et al., 1984; De Renzi et al.,

1989b; Vallar et al., 1994; Weinstein, 1994; Di Pellegrino & De Renzi, 1995; Milner, 1995) has been treated with controversy in the relevant literature.

According to our theory, desynchronisation due to unilateral slowing down of neuronal processing is a by-product of stroke. We have claimed that unilateral neglect is a non-specific manifestation of desynchronisation. Consequently, extinction will be defined here as the milder and related form of neglect and based on the same neuropathological mechanism.

Evidence for this interpretation has been provided by a study of Rorden et al. (1997). It was demonstrated that there are disruptions in the temporal dynamics of information processing in extinction patients. Rorden et al. (1997) have shown that a contralesional stimulus had to precede the ipsilesional one by over 200 ms to be reliably judged as coming first.

Dissociations between neglect and extinction could be associated with the severity of desynchronisation. The less severe the neglect symptoms, the more likely it is that the patient displays extinction phenomena. It is further predicted that the incidence of extinction in non-neglect stroke patients should be relatively high.

De Renzi et al. (1984) investigated the incidence, severity and persistence of auditory and visual extinction in a large group of unilaterally brain-damaged patients who were tested almost exclusively within the first three days of hospitalisation. The tests were repeated every three to five days until extinction could no longer be elicited on two consecutive sessions. The results showed that 46% of the 144 patients suffered from auditory extinction. After 30 days, auditory extinction was still present in 38% of the patients. One hundred and two patients were tested to investigate the relationship of visual to auditory extinction after excluding patients with visual field defects. Forty nine percent suffered from neither impairment, 19% of the patients displayed symptoms of auditory but not of visual extinction, 12.5% had impaired perception of bilaterally presented visual stimuli but no deficit in the auditory modality and, finally, 4% of the patients suffered from both visual and auditory extinction. These figures were replicated by Vallar et al. (1994) who tested their patients for visual and tactile extinction within 30 days of the cerebral trauma. Out of their group of 159 patients with unilateral brain damage, 71% had no extinction

symptoms, 13% displayed signs of tactile extinction, 9% of the patients suffered from visual extinction and 6% showed extinction symptoms both in the visual and tactile modality. Much higher figures for the incidence of tactile extinction were reported in a study by Schwartz et al. (1979). Sixty four percent of patients out of a group of unilaterally brain-damaged patients were diagnosed as suffering from extinction symptoms in the tactile modality.

While neglect appears to be much more frequent after right hemisphere damage (but see Ogden, 1985b, 1987), a comparable strong association does not seem to exist for extinction. Schwartz et al. (1979) examined 234 patients with unilateral cerebral damage. Extinction was associated with right hemisphere trauma in 70% of the cases compared to 59% after left hemisphere damage. The difference did not reach significance (however, the differences went in the same direction as in neglect). A similar result was obtained by De Renzi et al. (1984). Fifty two percent of right hemisphere patients displayed signs of extinction and as many as 40% of the patients after left hemisphere damage extinguished one stimulus on bilateral presentation. Critchley (1949), too, observed a slightly higher, though not significantly higher, incidence of tactile extinction after right hemisphere damage.

One possible explanation for the relatively equal distribution of left and right extinction might be the fact that the degree of slowing down which is required to cause extinction is much smaller compared to neglect. In other words, extinction is a much more sensitive measure of slowing down than neglect. Therefore, extinction emerges more often after left hemisphere damage compared to unilateral neglect. For unilateral neglect to become manifest, it takes a considerable degree of desynchronisation. The left hemisphere might be more robust than the right hemisphere where coarse coding is implemented to a greater degree.

6.2.1.9. Cross-over effect

The so-called cross-over effect refers to a phenomenon that emerges in line bisection tasks: The ipsilesional displacement of the midpoint becomes increasingly smaller for lines of decreasing length until the neglect patient eventually marks the midpoint on the contralesional side with respect to the objective centre of the line. Bisiach et

al. (1983) were the first to provide data on the cross-over effect (although it was not discussed as such by the authors).

One of the accounts put forward came from Chatterjee (1995) who interpreted cross-over as "resulting from a lack of inhibition of leftward confabulatory mental representations" (Chatterjee, 1995, p.455).
The claim of an imbalance between inhibitory and excitatory mechanisms after stroke is plausible. "The post-ischemic brain is a complex mosaic of very different metabolic and hemodynamic focal situations" (Fieschi, 1980, p.431).
A clinical manifestation of disinhibition is post-stroke seizures. Arboix et al. (1997) reviewed the notes of 1220 stroke patients and reported that early (within 48 hours post-stroke) epileptic seizures were diagnosed in 2% of the patients following ischemic stroke and 4.3% of patients who had suffered a cerebral bleed. Burn et al. (1997) set the risk of single or recurrent seizures in the first five years after stroke at 11.5%. Interestingly, Fukujima and Cardeal (1997) described focal slowing of cerebral activity in the EEG as the most frequent EEG pattern in post-stroke seizure patients. Furthermore, Romaniak and Baranaska-Gieruszczak (1998) reported diffuse slowing of background activity as an indicator of increased risk of seizure recurrence. As was described above, diffuse slow-wave bands are more pronounced in neglect patients compared to non-neglect stroke patients (Watson et al., 1977; Demeurisse et al., 1998). This observation would allow the hypothesis that there might be a higher degree of disinhibition in neglect patients.

Monaghan and Shillcock (1998) developed a computational model of performance in the line bisection task that produced a cross-over effect after unilateral damage. The model instantiated the concept of 'confabulation' released by disinhibition as proposed by Chatterjee (1995).
After being lesioned, different levels of noise were introduced into the network to mimic disinhibition. By varying the level of noise, differences between cross-over patterns could be produced that resembled the variations observed in individual neglect patients (Chatterjee, 1995). It was demonstrated that the higher the level of noise in the lesioned site, the longer the lines where cross-over emerged.

We will now try to apply the claims of our theory to the above findings. We have suggested that synchronisation between hemispheres and within the lesioned hemisphere is disrupted. How would this account for the cross-over phenomenon?
Let us make two general points: First, the cross-over effect emerges in shorter rather than longer lines and displacement of the bisection point increases as the line gets even shorter. In other words, the size of the stimulus determines the cross-over point. Second, it appears that the level of inhibition also determines when cross-over occurs. Let us suggest further that the level of disinhibition might be higher in neglect than non-neglect patients.

We hypothesis that cross-over marks the point where the opposing forces of two effects are equal: First, the effect which the size of the stimulus in the intact hemisphere exerts on interhemispheric interaction, and, second, the effect of confabulation caused by disinhibition in the damaged hemisphere.
It was illustrated earlier that the level of conscious processing in the lesioned hemisphere is improved when processing in the intact hemisphere is reduced (Arai et al., 1997; Beis et al., 1999). In other words, the performance in the lesioned hemisphere becomes better when the interference between rivalrous ipsilesional and contralesional representations decreases. This behaviour is in contrast to the so-called redundancy gain effect in normal processing. Some tasks are performed better when the processing load is distributed across both hemispheres (Hellige, 1990). Such a between-hemisphere advantage is often revealed when the target is presented to each hemisphere simultaneously (redundant target condition) compared to single target presentation (Davis & Schmitt, 1971; Hellige et al., 1989; Eng & Hellige, 1994; Mohr et al., 1994; Minussi et al., 1998; Hasbrooke & Chiarello, 1998) and has even been documented in blindsight patients (Marzi et al., 1986; Corbetta et al., 1990b). However, there is evidence from electrophysiological studies for the counterintuitive observation that the neglect patients' performance does not improve when stimuli are presented to both hemispheres simultaneously. Viaggiano et al. (1995) and Spinelli et al. (1994) investigated VEPs in neglect patients when stimuli were presented to each visual field separately or to both visual fields simultaneously. In normal subjects, a summation effect was reported: The response amplitude after simultaneous

stimulation of each visual field equalled the sum of the amplitudes of each separate visual field. In contrast, the response of neglect patients to bilateral stimulation was similar in amplitude to the response of either hemisphere alone. The data can be interpreted in three ways: Either, the intact hemisphere inhibited the damaged hemisphere so that processing in the contralesional hemisphere was suppressed. Or the neuronal activity was delayed to the extent that it was not recorded by the VEP measurements. Alternatively, the two mechanisms were both in place. In short, whatever mechanism is the underlying reason for the lack of summation in neglect patients, the data suggest that the nature of the interhemispheric interaction is altered in those patients.

The concept of desynchronisation could account for the cross-over in the following way: Lack of intrahemisheric synchronised activity produces only a weak electrophysiological representation of an object in the damaged hemisphere. The decrease of electrophysiological signature reduces its saliency. Furthermore, lack of interhemsipheric activity leads to the representation in the damaged hemisphere which is out of synch with the representation in the intact hemisphere. The combination of these two mechanisms will lead to the loss of the weak and delayed representation in the damaged hemisphere. Active suppression by the intact hemisphere does not have to be postulated.

The electrophysiological signal of the contralesional representation is stronger than in the ipsilateral due to preserved synchronisation. However, as the stimulus becomes smaller, the degree of activity decreases. Eventually, there is a point when activity in the intact hemisphere is so small that the level of activity in the damaged hemisphere is higher due to disinhibition.

The hemispheres are still out of synch but a reversal of conscious perception occurs. It is now the weaker representation in the intact hemisphere that is temporally incompatible with the stronger electrophysiological signal in the damaged hemisphere. Two mechanisms determine the cross-over effect: Neglect of the ipsilesional side and confabulation in the contralesional space.

7. Summary and conclusion

By postulating impaired desynchronisation as a plausible sequela of stroke, we have offered a parsimonious model that accounts for many aspects of unilateral neglect. However, our theory is not the first to associate abnormal temporal processing with a neuropsychological disorder. For example, Merzenich et al. (1993) reviewed the evidence of longer than normal integration and segmentation times in children with learning disability and dysphasia including some autistic and schizophrenic subjects. Likewise, Tallal et al. (1993, p.36) summarised: "Some children have a severe developmental deficit in processing brief components of information that enter the nervous system in rapid succession, and a concomitant motor deficit in organizing rapid sequential motor output. Importantly, this deficit appears to be highly specific, impinging primarily on neural mechanisms underlying the organization of information within the tens of millisecond range. The neurobiological basis of this deficit is, as yet, unknown. However, this deficit appears to account for the pattern of aberrations in the development of several aspects of higher level cognitive processes that are know to characterize children with developmental language and reading impairment". Llinás (1993) proposed to interpret developmental dyslexia as 'dyschronia' caused by cellular dysfunction. In this framework, the brain of dyslexics is incapable of creating time windows whose temporal resolution is high enough to cope with rapid on-line information (see also Hari & Kiesila, 1996).
Impaired temporal processing has also been reported in patients with acquired disorders. It has been suggested that nonfluent Broca aphasics have retained the ability to access lexical information automatically. However, Prather and her colleagues proposed that the patients' problem lies in a slowed activation process. (Prather et al., 1991, 1992, 1997). Also the catastrophic effects of slowed sensory-motor processing are illustrated by the disabilities of Parkinson's disease patients (Ashe & Georgopoulos, 1993) who are also known to suffer from neglect (Villardita et al., 1983).

To conclude, we have proposed desynchronisation of neuronal activity within the damaged hemisphere and between hemispheres as the underlying mechanism of unilateral neglect. As complete hemispherectomy fails to induce a substantial neglect

syndrome (Smith, 1974), we claim abnormal interhemispheric interaction (Spinelli et al., 1994; Viggiano et al., 1995), more specifically, interhemispheric incompatibility of information as the crucial factor triggering unilateral neglect. The intact hemisphere suppresses the damaged hemisphere whose neuronal signal is already decreased due to intrahemispheric desynchronisation. Other examples of suppression of incompatible information can be found in amblyopia, binocular rivalry and saccadic suppression.

As the impairment due to desynchronisation is unspecific of particular neuroanatomical structures, the deficits can arise at the 'lowest' sensory levels up to the most central levels of cognitive information processing. Our claims have therefore the power to unify a wide range of neglect theories that have been proposed in the past. However, our model provides a qualitative account of neglect. It does not offer quantitative predictions as Halligan and Marshall (1989), Smith (1994), Chatterjee (1995) or connectionist models have done (Mozer & Behrman, 1990; Monaghan & Shillcock, 1998; Pouget & Sejonowski, 1995, 1996, 1999).

Chapter Five

Time perception and the time bisection paradigm in unilateral neglect

This chapter will present the first experiment of the thesis, the time bisection paradigm. Recently the time bisection paradigm has been used in studies that have examined the time perception of stroke patients with frontal lesions (Nichelli et al., 1995) and of subjects with cerebellar degeneration (Nichelli et al., 1996). Here, for the first time, the time bisection technique will be applied to test neglect patients. The idea behind the experiment is to demonstrate that the processing speed is more slowed down in the damaged hemisphere of a stroke patient than it is in normal subjects. We will begin by discussing the theoretical background of psychological time and time perception.

1. The perception of time

Subjective time is one of the crucial dimensions humans use to orient themselves in the world. Despite its significance, there has been no sense organ found to be responsible for the perception of time (Zakay, 1990).

Gibson (1975, p.295) succinctly expressed the problem that researchers engaged in the field of time perception have to face: "There is no such thing as the perception of time, but only the perception of events and locomotions". What is it then that we experience and remember as the passing of time? Fraisse (1963, p. 234) proposed that "direct judgements [are] founded immediately on the changes we experience and later on the changes we remember".

There are three major aspects of psychological time that characterise the perception of our personal time and these have to be separated strictly from time in the macrophysical sense: Succession, temporal perspective and duration.

- ***Succession*** refers to the fact that two or more events are processed as distinct from each other and ordered sequentially to each other. Or put simply, events are perceived as successive when they are not perceived as simultaneous any more. Again it has to be stressed that perceived simultaneity is different from physical simultaneity (Fraisse, 1984). Hirsh and Sherrig's influential study (1961) demonstrated that the succession order threshold, regardless of the sensory modality, was constant at about 20 ms. The data were collected after long training sessions. However, Hirsh and Fraisse (1964) showed that untrained subjects displayed higher thresholds when a forced choice on the order of a sound and light stimulus was required. The threshold was around 60 ms when the auditory stimulus preceded the sound, and between 90 to 120 ms when the light preceded the sound. Also, for stimuli that are complex the threshold seems to be much higher than for simple stimuli (Fraisse, 1984). These data demonstrate that perception of succession is not a uniform mechanism but that it depends on different factors (e.g. the type of the stimuli, number of training sessions, modalities involved etc.).

- ***Temporal perspective*** describes the way in which the individual with him/herself as reference point connects to events in the past, present and future. This aspect of time perception is not relevant in our context and is mentioned for completeness.

- ***Duration*** refers to the time interval between two successive events. "Duration has no existence in and of itself but is the intrinsic characteristic of that which endures" (Fraisse, 1984, p.2). The threshold of perceived duration marks the ability of an individual to distinguish the on- from the off-phase of a stimulus (Fraisse, 1984). Before this distinction is achieved, an event is perceived as instantaneous rather than enduring. Studies applying psychophysical measurement methods have established an instantaneity threshold of 60 ms with a range of uncertainty from 30 to 130 ms (Servière et al., 1977a). Here again, when naïve subjects were tested the threshold was higher than in trained test subjects. In evoked potential studies, Servière et al. (1977b) demonstrated that the on- and off-components of the stimuli were perceived as clearly distinct beyond a 140 ms threshold. Below this value, a range of uncertainty could be established which was similar to the one found with psychophysical techniques.

Fraisse (1984) emphasised an often overlooked distinction of two types of processing in the evaluation of duration on the grounds that different psychological mechanisms are involved. The perception of the duration refers to the perception of the psychological present whereas the estimation of duration involves memory processes.

2. The duration of time

2.1. The perception of duration

The concept of the psychological present was first introduced by William James (1890) under the term of "specious present". He illustrated his idea with the picture of "a saddle-back ... on which we sit perched, and from which we look into two directions into time" (James, 1890, p.609, vol.1).

The psychological present is defined as the time interval within which the sequence of events are analysed simultaneously by the perceptual and cognitive systems, or in other words, events of the psychological present are characterised by their "availability to our attention in real time" (Michon, 1978, p.91).

Opinions about the width of this time interval vary. Pöppel (1994) postulated a temporal window of approximately 3 s as psychological present. Fraisse (1984) proposed an average value of 2 to 3 s and considered 5 s as upper limit. Block (1979) proposed an upper limit of 5 s and Michon (1978) of 7 or 8 s, whereas Zakay (1990) quoted a figure ranging between 500 ms and 700 ms .

Neuropsychological evidence, however, lends support to Fraisse's estimation of the psychological present. Elbert et al. (1991) used the method of event-related potentials to investigate time processing mechanisms. Subjects were presented with visual stimuli on a screen for intervals of varying length. The subjects were then asked to reproduce the length of each interval. During the trials, the event-related potentials were measured. The results suggested that there is a qualitative difference in the processing mode when intervals of up to 4 s are reproduced compared to intervals longer than 4 s.

Different authors have equated the psychological present with concepts like "very short term-memory" or "short-term memory" (Fraisse, 1984, p.10). However, Michon (1978) rightly pointed out that the maximum length of the psychological

present cannot easily be compared with the 20 to 30 s range which is usually found in short term memory tests.

Segmentation is another organisational principle of the present, apart from attentional availability. This appears to be the reason for the relatively wide range of time intervals stretching across the present. The information stored in the present forms a discrete unit. The boundaries of this unit are influenced by temporal and non-temporal structural factors. If there is no external structure provided by the stimulus, segmentation of the stimulus will be achieved subjectively. The duration of the segmented unit of information can therefore vary depending on its internal and external structural properties. As soon as segmentation is completed, i.e. some structural boundary is reached, the information segment will be relayed for higher order analysis and a new present will commence (Michon, 1978).

The methodological relevance of the above discussion is that studies which examine duration perception should limit their tests to time intervals between approximately 100 ms to maximally 7 s. If however the investigated time range exceeds 7 s (some authors would only accept 3 to 5 s as upper limit), the obtained data cannot be compared with each other, as different psychological processes are involved.

2.2. The estimation of duration

If the limits of the perceived present are exceeded, duration can only be estimated by involving short- or long-term memory. When we estimate a perceived duration, an event of the immediate past is connected with one in the far past or two events of the far past are compared with each other. Again this has important methodological consequences.

To summarise, there are three different orders of duration on the physical continuum:

a) Shorter than 100 ms at which the perceived event is instantaneous.
b) 100 ms to 5 (7 s) during which the psychological present is perceived.
c) Above 5 (7 s) at which the estimation of duration activates memory processes (Fraisse, 1984).

In the next section, we will discuss various models of temporal processing. Models analysing perception of successive events and temporal perspective will not be mentioned as they are not relevant to the framework of this thesis.

3. Models of time perception

In this section various models of time perception will be discussed (no explicit distinction will be made between perception and estimation of duration as outlined above). The presentation is by no means comprehensive. It is only intended to give an overview of the existing theories.

There are two approaches to temporal processing: The classical methods of the psychophysical tradition and the more recent cognitive analyses. Allan (1992) has advocated the integration of the two approaches rather than the replacement of the former by the latter direction.

3.1. Psychophysical models

The goal of the classical tradition of time perception was to investigate a subject's reaction to 'pure' time. Content-free stimuli were used as markers of the judged durations. Models which emerged from this framework of thinking used an internal clock concept which was based on psychophysical relations like the psychophysical law and Weber's law (Allan, 1992).

3.1.1. The psychophysical law

There are two main issues in the discussion of the perception of 'pure' time: First, the nature of the relationship between mean subjective time and real time which is expressed by the psychophysical law. Second, the relationship between mean subjective time and variability of subjective time which is described by Weber's law.

The relationship between the intensity of the perceived stimulus and the magnitude of the physical stimulus has been investigated since Fechner. Early researchers interpreted their results following Vierodt's law which states that short intervals are overestimated and long intervals tend to be underestimated (with the indifference interval being the time duration which is neither over- nor underestimated). Woodrow's work (1930, 1933, 1934) showed that time perception was not governed by Vierodt's law.

The debate continued while various researchers attempted to prove that the relationship between perceived stimulus and the force of the external stimulus could

be described by a power law (e.g. Eisler, 1975). Controversy existed over the magnitude of the duration exponent. Some studies reported exponents of the power function of well above 1.0 (Björkman & Holmkvist, 1960; Frankenhaeuser, 1960), Stevens (1967) proposed a value of 1.0 which means that perceived time is in a linear relationship with physical time. In Eisler's study (1975), an average exponent of 0.84 emerged. Eisler (1976) reviewed the relevant duration experiment literature and derived an average exponent of 0.9. Also, there appears to be a significant difference between subject variability (Eisler, 1975) and between experiment variability (Eisler, 1976; Allan, 1979). Furthermore, Allan (1978) demonstrated that the same exponent values do not apply to the different experimental paradigms in time perception.
In summary, it is still disputed whether perceived time and physical time can be adequately described by a psychophysical law.

3.1.2. The Weber's law model of Getty

Getty (1975) introduced his Weber's law model which investigates the relationship between mean subjective time and the variability in subjective time.
The basic Weber's law claims that the just noticeable difference ΔT is a constant proportion, k_w, of the standard duration T. Weber's law is given as:

(1) Standard Deviation (T) = $k_w T$ where k_w (> 0) is the Weber fraction.

If Weber's law holds, the variance of the function will increase as the square of T:

(2) $Var_w(T) = (k_w T)^2$

The Weber fraction $k_w = SD(T)/T$ should remain constant independent of T.

Getty's work (1975, 1976) developed a generalisation of Weber's law and presented the strongest evidence in support of its predictions. The model was motivated by the attempt to accommodate some data which were not reconcilable with Weber's law. There was evidence that the Weber fraction did not remain constant for very short durations and very long durations. Blakeley (1933; cited by Getty, 1975) derived a Weber fraction which was a U-shaped function of standard duration. The fraction remained relatively constant for durations between 0.2 s to 1.5 s but increased beyond both of these boundaries. Similar data were reported by Stott (1933; cited by Getty, 1975). Various other duration discrimination studies (Abel, 1972a,b; Allan et

al., 1971; Creelman, 1962; Small & Campbell, 1962) demonstrated an increase of the Weber fraction for time durations below 200 ms. A constant sensory noise component, independent of the value of the stimulus, was commonly considered to be the cause of the Weber fraction deviation.

Getty (1975) claimed that the variability in discrimination tasks emerged from different sources: One which is dependent on the magnitude of the stimulus and one which is independent of the value of the stimulus. He further assumed a mutual independence of these sources which led him to propose that the total variance is the sum of the component variances, V(T) which is the magnitude-dependent variance, and V_R which is the magnitude-independent residual variance of constant value.

(3) $\mathrm{Var}(T) = V(T) + V_R$

If V(T) obeys Weber's law from equation (2), it follows from (3) that

(4) $\mathrm{Var}_w(T) = k_w^2 T^2 + V_R$

and

(5) $SD_w(T) = (k_w^2 T^2 + V_R)^{1/2}$

The generalised Weber fraction is derived from (5):

(6) $SD_w(T) / T = (k_w^2 + V_R/T^2)^{1/2}$

This function can account for the increased Weber fraction for short time intervals reported in the above studies (Abel, 1972a,b; Allan et al., 1971; Creelman, 1962; Small & Campbell, 1962; Stott, 1933; Blakeley, 1933, cited by Getty, 1975). As the time interval becomes longer, the Weber fraction decreases quickly and becomes a constant for durations up to 2 s (Getty, 1975). Getty (1975) conceded, though, that his equation could not explain a steep rise of the Weber fraction for time durations exceeding 2 s.

In summary, models of duration perception based on Weber's law still remain controversial with Getty's model (1975, 1976) being successful in accounting for some of the discrepancies in the data.

3.1.3. Creelman's counting model

Hoagland (1933; quoted by Block, 1990) postulated a master chemical clock that governs time-related behaviour and time perception. "The proposed mechanism is somewhat analogous to the modern conception of biological rhythms in that it relies

on the notion that activity in certain parts of the brain underlies psychological time" (Block, 1990, p.15). However, Hoagland did not specify which brain area was supposedly involved in the time-related function. So far neuroanatomical data have not supported Hoagland's concept of a chemical clock, other than the processes involved in circardian rhythms (Block, 1990).

More recently, also without speculating about a possible biochemical or neural substrate, Creelman (1962) developed the first quantitative model for duration discrimination which extended Hoagland's ideas (1933). The model assumed that human subjects discriminate time durations by 'counting' input pulses during the duration to be judged. "It is sufficient for the moment to view the source of pulses as a large number of independent elements whose time of firing is randomly distributed" (Creelman, 1962, p.590). λ represents the probability that a given element in the pulse source will fire during a given interval T. Therefore, the mean number of counts produced will be λT for the duration T and $\lambda(T + \Delta T)$ for the duration $(T + \Delta T)$. The distribution of the number of accumulated pulses follows the Poisson law which is closely approximated by the normal distribution with a large λT.

According to Creelman (1962), the decision rule the subject applies to arrive at the correct distinction between a short and a long interval is simple: The duration $(T + \Delta T)$ is of longer duration than the interval T if the standard deviation of the input pulse count $\lambda(T + \Delta T)$ is greater than the standard deviation λT.

However, as Allan et al. (1979) pointed out, the predictions of the counting model were not confirmed. Most results that were examined within the Creelman framework demonstrated that λ was not constant across different time intervals (e.g. Abel, 1972a,b; Allan et al., 1971).

3.1.4 Other internal clock models

Treisman (1963) also did not enter into the discussion as to where the neurophysiological correlate was to be found in the brain when he proposed a general

theory of time perception. The components of his "internal clock" model are illustrated in figure 1.

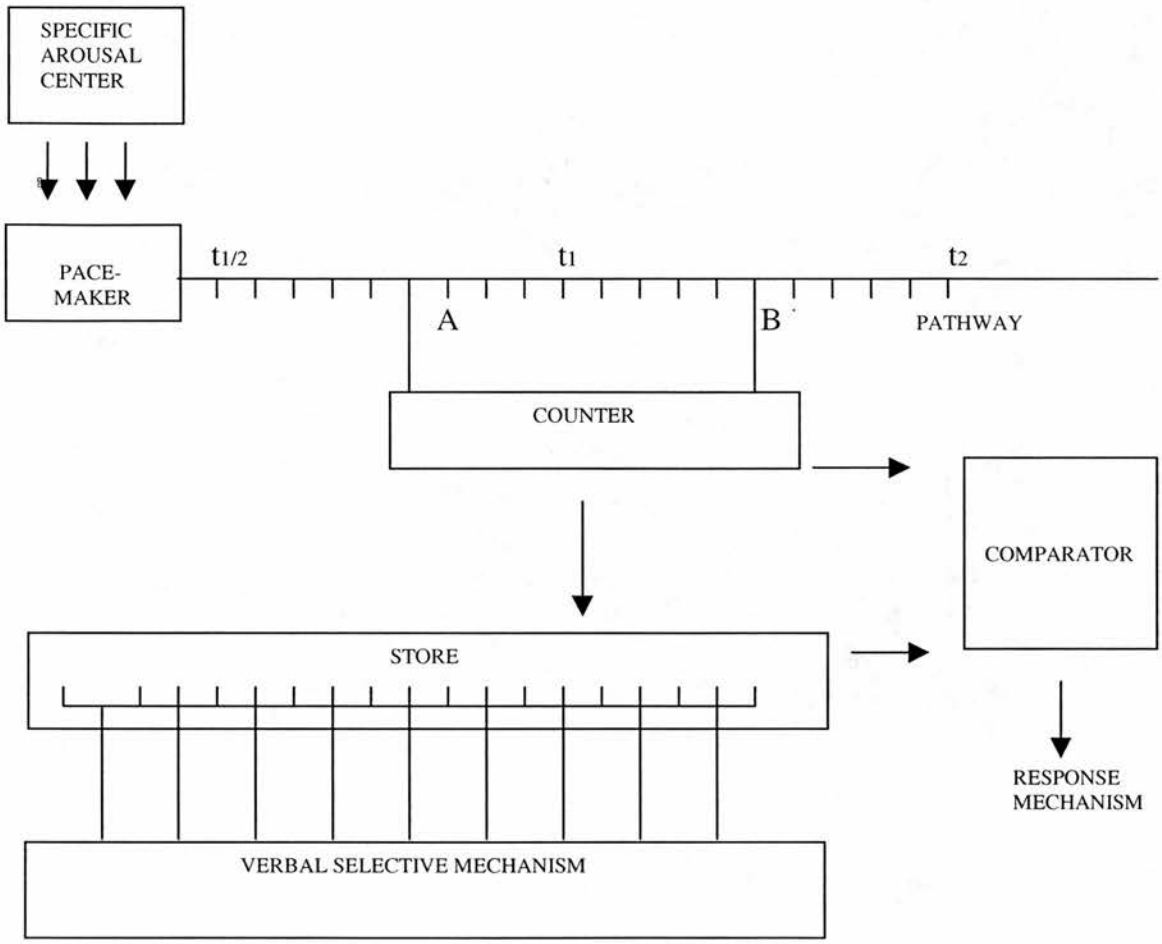

Fig. 1: Internal clock model

This model consists of the following components: The pacemaker generates pulses at a regular rate which travel along the pathway. The rate of the pacemaker can be modified by the specific arousal centre.

A counter accumulates and counts the number of pulses and relays the value of the pulse count to the store. The comparator is the "decision mechanism" of the model (Treisman, 1963, p.19). It can retrieve stored information from the store and also receives the pulse count of the most recent stimulus duration which it then compares. A "verbal selective mechanism" (Treisman, 1963, p.19) which acts as a long-term

memory story (with labels such as 15 s, 2 min etc.) influences the store and enhances retrieval.

Another model in the tradition of the internal clock is the scalar timing theory first proposed by Gibbon (1977). Gibbon's theory will be explained in detail in the following section as the experimental paradigm used in our study is based on the scalar timing theory.

3.2. Cognitive models

Block (1990), an advocate of the cognitive approach to temporal processing, criticised internal clock models as "an oversimplified view of the complex set of processes that underlie psychological time" (Block, 1990, p.18). Accordingly, these models fail to account for the fact that cognitive factors like attention or non-temporal factors can influence time-related behaviour. The components of internal clock models appear relatively autonomous and shielded from internal and external factors (Block, 1990). Allan (1992) on the other hand conceded that these models have their limitations but stressed their theoretical importance and advocated the integration of the two approaches instead of replacing the traditional views with the more recent cognitive analysis. Three models in the cognitive tradition of time perception will be presented below.

3.2.1. The attentional allocation model of time perception

The so-called interference effect refers to the observation that for subjects when they are asked to perform demanding non-temporal tasks the perceived time becomes shortened (for a review see Zakay & Block, 1996; Brown, 1997). A number of researchers have proposed an attentional allocation model to account for the phenomenon (e.g. Thomas & Weaver, 1975; Thomas & Cantor, 1975, 1978).

The attentional allocation model presumes that temporal processing requires the allocation of attentional resources. The more attention there is available for time processing, the longer the perceived duration. The lengthening of perceived time might be mediated by enhanced accumulation of temporal cues in a cognitive timing mechanism. Similarly, if there is no time allocated to time processing because the

resources are used up by non-temporal task demands, fewer temporal cues are accumulated in the timer due to loss or incomplete processing. The result is "an internal temporal record that is incomplete, unreliable and full of gaps. Time judgements, based on this record, are correspondingly inaccurate. These judgements often show that perceived time is shortened" (Brown, 1997, p.1120).

The attentional allocation model offers a clear explanation of the interference effect. However, the account has been criticised for assuming that attention is allocated evenly and does not fluctuate. In other words, the level of alertness, concentration, moods or other cognitive processes are not taken into account (Block, 1990). Also, Block (1990) criticised the use of terms like "attention to time" and "temporal information processing" as too vague.

3.2.2. A memory storage model

Philosophers of the antiquity contemplating the nature of time-related experiences claimed a close connection between the perception of time and memory-related processes. Aristotle in 330 BC postulated that "only those animals which perceive time remember, and the organ whereby they perceive time is also that whereby they remember" (McKeon, 1941, pp.607-608; cited by Block, 1990).

In more recent times, specific memory-based models have been developed, among which we will discuss Ornstein's theory (1969). Ornstein (1969) criticised internal clock models because they could not account for the fact that the mechanisms involved in encoding information have an influence on remembered duration. In Ornstein's view, remembered duration is a cognitive representation which is determined by what he called the *memory storage size.* Thus, "the experience of duration of an interval is a construction formed from its [neurological] storage size ... As storage size increases, duration experience lengthens... If the reverse ... is attempted ... storage size should be reduced and duration experience should be shortened... " (Ornstein, 1970, pp.42,43; quoted by Hogan, 1978). In other words, when an individual encodes more information during a certain time interval or if he/she processes that information in a more complex way, the experienced duration of this time interval increases. Time perception is therefore linearly and positively connected to stimulus and processing complexity (Hogan, 1978; Block, 1990).

Block (1978) contested Ornstein's position (1969) in an experiment which showed that the complexity of a stimulus event only had partial effects on remembered duration. Subjects were asked to view two sequences of slides and to pay attention to the pattern. Then, unexpectedly, they were asked to make a comparative judgement of the duration of the two intervals. Only one out of two experiments revealed an association of stimulus complexity with the increased perception of time intervals.
As an alternative to the memory storage model Block and his colleagues (Block, 1978; Block and Reed, 1978) proposed a theory which focused on the changes of the cognitive context, an approach that had been suggested earlier by Fraisse (1963).

3.2.3. The contextual change model

In a series of studies (Block, 1978; Block & Reed, 1978; Block, 1982), evidence was presented for the fact that contextual changes in information processing and in the environment influence remembered duration. These contextual changes of information processing include background stimuli, interoceptive stimuli (e.g. posture, temperature, nausea), psychological states like moods or emotions and cognitive strategies (Block, 1990). Changes in the environmental context are previous experiences in a room for example (Block, 1982).
To accommodate these findings, the so-called contextual change model of remembered duration was introduced (Block, 1978; Block & Reed, 1978). According to this model, contextual information rather than stimulus information is an integral part of memory encoding of events. Accordingly, when a duration is remembered, contextual information is accessed and retrieved to create a cognitive reconstruction of the duration of this event.
Two versions of this model exist. In the first one, it is claimed "that the critical factor is the number of different contextual associations connected with the memory traces of stimulus events" (Block, 1990, p.25). The model in this form had to be discarded after Block (1986) demonstrated that subjects remembered an imagery task that involved a large number of different contextual associations as being shorter, rather than longer, compared to an imagery task with few contextual associations.
However, a weaker second version of the model was still upheld according to which "an overall change in context from a preceding duration to the to-be-judged duration,

which is encoded during the to-be-judged duration is the critical factor underlying the remembered duration" (Block, 1990).

There are a number of problems with this model. For example, there is no independent way to measure the degree of change in the contextual context. Furthermore, no reliable method exists to determine and control which cognitive process(es) is/are involved every time a person tries to remember the duration of a time interval.

We will now proceed to discuss the different methodological approaches and dangers with the study of the perception of psychological time.

4. Studies of time perception: Methodology and pitfalls

In quantum physics, measuring the states of quantum particles is often a futile undertaking. The obtained information provided by the measurement never reflects the quantum state the particle was in before the measurement was taken. That is, the act of measuring interferes irreversibly with the dynamics of the quantum particles (e.g. Buchanan, 1998). According to Zakay (1990), there is a unsettling parallel in the study of time, "the domain in which modern physics and psychology meet" (Zakay, 1990, p.81). Similarly, time is an entity which will be influenced by the conditions under which it is measured. This situation demands a most thorough methodological approach and does not allow to make quick generalisations from the results of different studies. In this section, we will address important methodological aspects of time studies and their potential pitfalls.

4.1. Methods of time perception studies

There are a number of different techniques to investigate the perception of time. Each method taps different time-related processes that yield different results. Zakay (1990, p.63) indicated four basic methods of time perception:

1. "Verbal estimation: The target interval duration is estimated verbally in terms of temporal units.
2. Time production: A predefined interval of a given length is produced.
3. Reproduction of time: The target interval is reproduced by means of some operation.

4. Comparison: Two intervals are presented and the estimator is to judge which is longer."

A more elaborate list was proposed by Nichelli (1996, p.190) (see table 1).

Table 1: Methods used in time perception studies.

Duration Scaling	**Duration Discrimination**
1. Temporal Production	1. Comparison
2. Synchronisation	2. Single Stimulus
3. Magnitude Estimation:	3. Time Bisection*
- Verbal Estimation	
- Estimation by analogical comparison	
4. Category Rating	
- Time Bisection*	
- Temporal Generalisation	
5. Ratio Setting	
- Temporal Reproduction	

(*) The different classifications of the time bisection paradigm will be explained at a later stage.

4.1.1. Duration scaling

In temporal production experiments the subject is required to produce a time interval of a fixed duration (e.g. 3 s or 9 s). The interval can be generated by two single responses marking the start and the end of the interval. Alternatively, the subject produces a time interval with a single response (e.g. sustained button press). The degree of feed-back can vary.

This method has been employed to investigate specific processing demands than can influence time perception. First the subjects practice to produce an interval of specific duration. Then they are trained in a different task. It is then investigated what effect this concurrent non-temporal processing has on the perception of the fixed interval.

Synchronisation is related to time production. The subject is presented with a sequence of time intervals. He/she is then asked either to synchronise his/her response with a given stimulus or to continue the given sequence of intervals after the termination of the stimulus. Rhythmic tapping is an example for this paradigm. The subjects are presented with a sequence of isochronous short sounds. The task is to press a response key in synchrony with the given tones.

In the magnitude estimation task, a reference interval of fixed duration is given at the beginning of each trial. There are various forms in which an answer can be given by the test subject. In verbal estimation the response is given in conventional time units. A variation of magnitude estimation is when the subject makes an estimate by analogical comparison, by for example drawing a line.

In category rating the subject is asked to assign the response to one of "n" ordered categories. The most widely used form of category rating is the time bisection paradigm which has been used in the study reported below. It will be discussed in detail at a later stage in this chapter.

A second example of category rating is the temporal generalisation method. Here the standard interval is the only category according to which the test intervals have to be classified. Subjects are repeatedly presented with the standard interval. After the training phase the test intervals of varying durations are presented spaced in equal steps around the standard interval. The subject has to determine for each test interval whether it was equal to or not equal to the standard interval.

An example for ratio setting is the paradigm where the subject has to reproduce a given test interval.

4.1.2. Duration discrimination

In the comparison paradigm, subjects are presented with two durations sequentially. The response is a same/different decision. There are two versions of this experiment. The two stimuli can both vary. Or one of the intervals is fixed and serves as a standard stimulus. If the latter is the case, the standard interval can occur either first or second. The single stimulus paradigm is a method where the subject is presented with one of two possible duration values on each trial. The subject is asked to decide whether it was the shorter or the longer value. A particular version of the single

stimulus method is the time bisection experiment. In the next section, we will continue with the possible dangers in designing a time perception experiment.

4.1.3. Methodological pitfalls

4.1.3.1. Time order error

The order in which various time intervals of different lengths are presented has a bearing on the subject's performance. This effect is called the time order error. Most research on the time order error has been conducted in a paradigm where the subject has to make a forced choice about two intervals which are presented sequentially. Either the long interval follows the short one ($S_0 S_1$) or the short one follows the long one ($S_1 S_0$). The correct judgement of the intervals is expressed by two conditional probabilities:

(1) $P(R_{10} / S_1 S_0)$ and $P(R_{01} / S_0 S_1)$

R_{10} indicates the judgement that the longer interval preceded the shorter one, and R_{01} indicates that the longer interval followed the shorter one. The difference between the two conditional probabilities is called the time order error:

(2) $P(R_{10} / S_1 S_0) - P(R_{01} / S_0 S_1)$

The time order error appears to be duration dependent. In a positive time order error, the first of two equal time intervals is reported to be longer than the second one. The reverse applies for a negative time order error. For short durations, the time order error tends to be positive, for long ones negative (Allan, 1979). According to Zakay (1990) the estimation method also has an influence on the value of the time order error. For example, verbal estimation experiments appear to produce a negative time error, the analogical comparison by line length a positive time error and, in the reproduction paradigm, the time error has an unpredictable direction.

Opinion is split over the question during which stage the time order error is produced. Does it emerge at the level of perceptual memory as proposed by Woodrow (1935; quoted by Allan, 1979)? An alternative explanation has sought the time order error in the perceptual domain generated by adaptation and differential weighting processes of the sensation. A third view postulated the emergence of the time order error during the decision making process which causes a bias as a function of a particular task (Allan, 1979; Fraisse, 1984).

4.1.3.2. Memory processes

Different memory processes are involved in different experimental paradigms. For the estimation, the production and probably reproduction of short temporal intervals, processes involving short-term memory are crucial, since the response to the temporal stimulus is given immediately after its presentation.

"This, however, is not the case regarding the comparison method, unless the total time period, including the standard and the target intervals, is very short " (Zakay, 1990, p.66). Naturally, the question arises of which duration this short interval quoted by Zakay (1990) is and which definitions of short-term memory, working memory and long-term memory are applied.

The definitions and terminology of these different concepts are not at all clear. This is best demonstrated by two extreme views. Michon (1975; quoted by Zakay, 1990) attaches "the transition from immediate memory to short-term memory" (Michon, 1975, p.304) to the 500 ms boundary. This view is different from Fraisse's (1984) position. According to Fraisse (1984), "beyond the limits of the perceived present, duration can only be estimated by the subject's construct which brings to bear short and long-term memory" (Fraisse, 1984, p.30). In Fraisse's framework, the perceived present ranges from 100 ms to 5 s. Only beyond the threshold of 5 s, the estimation of duration involves memory processes according to Fraisse (1984).

4.1.3.3. Cognitive biases

It has been demonstrated that expectation and attention have an influence on the estimation of duration. For example, Edmonds et al. (1981) instructed his subjects that after the passage of a certain time interval either a pleasant, unpleasant or subjectively neutral experience would follow. The results showed that for the group with the positive expectation time passed more slowly compared to the two other groups where time passed more quickly.
An analysis which deals with the problem of how attention is divided between time perception and non-temporal information has already been presented above in Thomas and Weaver's model (1975) of time perception. The issue of the availability

of attentional resources to the test subject is of particular interest in a study which investigates time perception in neglect patients. Typically, the attention span in this kind of patient is very limited. It is the aim of this study to illuminate the question whether the attentional deficit could be an epiphenomenon of impaired time perception or an independent symptom of the pathology.

4.1.3.4. Time estimation strategies

Subjects might employ undesired strategies like chronometric counting. Zakay (1990) suggested that the instruction alone not to count might not be sufficient. On the contrary, the subjects' attention might be directed to this aspect of the experiment by the instruction. Engagement with a non-temporal task like the repetition of a word is often employed to prevent subjects from counting (see for example Nichelli et al., 1996).

4.1.3.5. Inducing time stress

Zakay (1990) warns about an experimental set-up that puts subjects under time stress. A stressful situation might make the subjects employ different methods and strategies to cope with the task compared to the problems which are encountered in a less stressful experiment.

4.1.3.6. Task complexity

The complexity of a task has a well known influence on time estimates. However, it is not easy to measure the relative complexity of the experiment. Information processing load, workload, attentional requirements, and time stress for example can contribute to complexity (Zakay, 1990). This is particularly relevant when working with different subject groups. A comparison between groups has to be done with caution, especially when subjects with neurological disorders and without pathologies are involved. It is therefore desirable, to minimise task complexity as much as possible in this case.

In the next section, we discuss how the nature of the stimulus can influence time perception.

4.1.3.7. The nature of the stimulus

The filled duration illusion describes the phenomenon that a filled interval is judged as longer than an empty interval of the same duration (eg. Steiner, 1968). Similarly, a temporal interval containing brief tones appears longer than an empty interval of the same duration (Thomas & Brown, 1974).

There are also modality differences in the perception of duration. A filled auditory interval is perceived as longer than a filled visual interval of the same stimulus duration (eg. Goldstone & Lhamon, 1974; Walker & Scott, 1981). This effect has been demonstrated in different tasks, with auditory stimuli of various intensities and frequencies and with visual signals of different intensities and wave lengths (Allan, 1979). Also, the more intense the stimulus which marks a time interval is, the longer the subjective duration (Fraisse, 1984).

The composition of markers of empty intervals appears to be important, too. Woodrow (1928) demonstrated that lengthening of either the onset- or the offset-marker caused an increase of the judged interval duration, in which the onset-marker had a more significant effect. Divenyi and Danner (1977), however, showed that stimulus durations of more than 80 ms were little affected by the properties of the markers.

The kappa effect describes the effect distance has on the perception of time. If two different sound sources are placed in space horizontally, separate from each other, and if two sequential sounds are produced corresponding to these two points in space, the distance of the sound sources has an effect on how long the time interval marked by the sounds is judged. The further apart the points are in space, the longer the judged time interval (Fraisse, 1984).

Thomas and Weaver (1975) showed that the duration during which a nonsense word is displayed tachistoscopically is judged longer than the display of a blank field of the same duration. Familiarity with the stimuli also seems to have an influence on perceived time. Avant and Lyman (1975) and Avant et al. (1975) showed that a three-letter non-word was judged longer than a three-letter word. A reversed result was reported by other studies (Devane, 1974; Warm et al., 1964; Warm & McCray, 1969). Their results indicated that the more familiar a stimulus, the longer its perceived duration will be judged (Allan, 1979).

In the following section, we will present the experimental paradigm that was used in the current study to investigate to what extent time estimation is impaired in stroke patients with and without neglect. It is predicted that subjective time will be processed differently in the damaged hemisphere.

5. The interval bisection paradigm

5.1. Scalar timing theory

The time bisection paradigm is rooted in the scalar timing theory, a model that continues the internal clock tradition. The scalar timing theory was first proposed by Gibbon (1977) and since further developed (Gibbon, 1981a,b; Gibbon & Church, 1984; Gibbon et al., 1984). It was an influential model in the animal timing literature but has found recent support for its application to human timing behaviour (Gibbon et al., 1984; Zeiler et al., 1987; Wearden & McShane, 1988; Wearden 1991a,b; Allan & Gibbon, 1991; Allan, 1992).

The bisection paradigm is a human analogue of a classical reinforcement experiment in the animal literature. A typical experiment with a rat is structured in the following way: During the training phase, the rat is exposed to two signals of different durations (e.g. 2 s. and 8 s). After the presentation of the signal, the rat is encouraged to operate two levers. Manipulation of one lever is reinforced with food after the short interval and response on the other lever is reinforced after the longer interval. The rat soon acquires a high degree of discrimination between the two stimuli. During the test phase the rat is exposed to various time intervals ranging between the short and long training interval without receiving any reinforcement. The responses at the two different levers, normally the response after the long training interval, is plotted against stimulus duration.

Similarly, human subjects are presented with a short and a long standard interval during the training phase of the interval bisection paradigm. In the test phase the subject is asked to classify intermediate interval durations as either closer to the short or long standard interval. Figure 2 (from Allan & Gibbon, 1991) illustrates the different constituents of the scalar timing model. This is a slightly modified version which was used by Allan and Gibbon (1991) to analyse their bisection data.

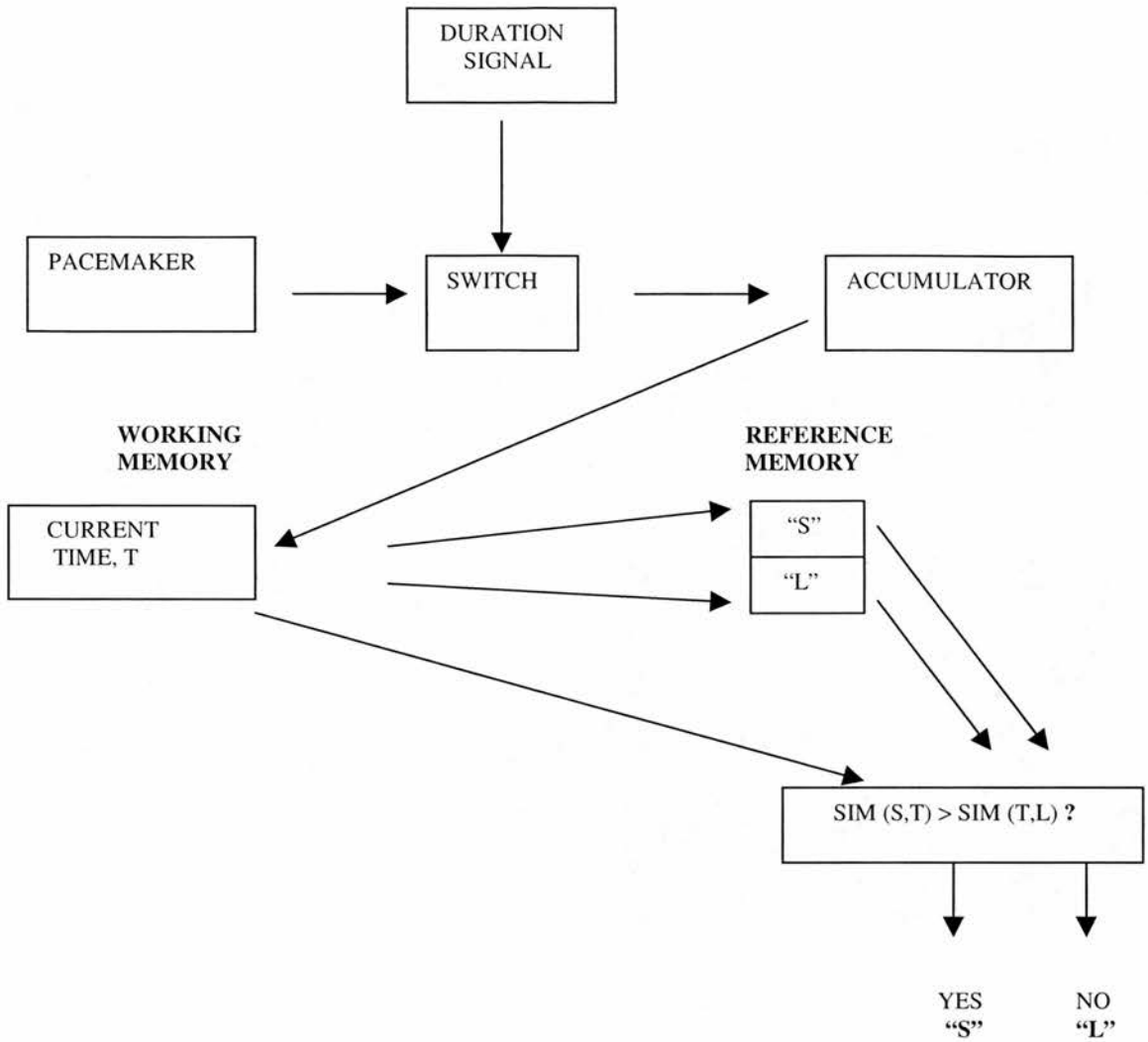

Fig.2: The scalar timing model (from Allan & Gibbon, 1991).

The clock part is made of a pacemaker, a switch and an accumulator. The pacemaker generates pulses at some rate. These pulses are accumulated by the accumulator through the switch which is opened by the timing signal. The pulse count of the accumulator is relayed to the working memory and its magnitude is compared to the stored value of the short (S) and long (L) standard intervals in the reference memory. The resulting values of these two comparisons which reflect the similarity of the current time interval T to the referents are then again compared in a ratio. The subject responds with "short" when the similarity of the current time interval T to the short standard interval S is greater than the similarity of T to the long standard interval L.

Each component of the model is a potential source of variance. It is postulated in the model that at least one of the sources of variance be scalar. The definition of a scalar

source of variance is one where the standard deviation of a process grows linearly with the mean of the process. Furthermore, it is claimed that the scalar sources of variance are larger than the non-scalar sources (Allan, 1992).

In Gibbon's full version (Gibbon et al., 1984) both constant and Poisson sources of variation as well as scalar sources are included. However, Allan and Gibbon's model (1991) used a version in which scalar sources of variance dominate the system which overrides the potential Poisson variation of a neural pacemaker and the constant variation in the gating switch operation. Allan and Gibbon (1991) adopted, consonant with Gibbon's model, a power exponent of 1 which means that mean subjective time is linear with real time and that the standard deviation of subjective time is linear with the mean of subjective time (the scalar property).

We decided to analyse our data within the framework of the scalar timing theory despite the criticism that cognitive factors like processing strategies or attention are not taken into account (Block, 1990). However, it has been a successful model of time-related animal behaviour in a variety of situations and there is now evidence that the scalar timing theory is applicable in the context of this particular paradigm, namely the interval bisection task involving human subjects (Allan, 1992; Allan & Gibbon, 1991; Gibbon et al., 1984; Wearden & McShane, 1988; Wearden 1991a,b; Zeiler et al., 1987). Two studies have recently applied the time bisection paradigm to examine stroke patients with frontal lesions (Nichelli et al., 1995) and subjects with cerebellar degeneration (Nichelli et al., 1996).

5.2. The neural systems associated with temporal behaviour

The psychophysical and cognitive models provide a conceptual framework to analyse time perception. However, the next step is to identify the neuroanatomical structures that are involved in timing behaviour (for a review see Ivry, 1996; Gibbon et al., 1997). Gibbon et al. (1997) proposed a complex striato-thalamo-cortico-cerebellar network. In the next section, we will present the main components of this network.

5.2.1. Cerebellum and pre-frontal cortex

Traditionally, the cerebellum has been associated with timing control (Braitenberg, 1967). The classical signs of cerebellar dysfunction, dysmetria and dysdiadochokinesia, have been interpreted as the patient's failure to time onset and offset of opposing muscle groups involved in a motor pattern (see e.g. Holmes, 1939, quoted by Ivry et al., 1988). Ivry and his colleagues (1988) demonstrated a dissociation of different parts of the cerebellum between timing and implementing movement. His group (Ivry et al., 1988) examined seven patients with cerebellar damage. Four patients had a focal lesion mainly in the lateral hemispheric region of the cerebellum. In three patients the lesion was mainly situated in the medial area of the cerebellum. The results showed that lateral lesions were associated with an impaired central timing process whereas patients with medial lesions displayed a deficit in implementing motor movement within the desired time frame despite the preserved judgement of when to make a response. Ivry et al. (1988) concluded "that the lateral regions of the cerebellum are critical for the accurate functioning of an internal timing system" (Ivry et al., 1988, p.167; see also Pellionisz & Llinás, 1982). A PET study provided further evidence for the involvement of the cerebellum in perceptual timing (Jeuptner et al., 1995). In this study, regional cerebral blood flow was measured in subjects listening to pairs of auditory intervals. The images showed an increase in regional blood flow in the cerebellar hemispheres during a temporal comparison task. No increase was reported in a control task where no perceptual events were involved.

Mangels et al. (1998) tested patients with unilateral focal cerebellar and pre-frontal lesions in two duration discrimination tasks while also manipulating the task demands with regard to attention and working memory. One set of test intervals centred around 400 ms and the other centred around 4 s. The data revealed the following results: First, cerebellar deficits led to impaired timing in both millisecond and seconds ranges whereas pre-frontal damage resulted in deficits only at the longer durations. Second, the processing of the cerebellum was not sensitive to manipulations of working memory and attention load whereas the performance of pre-frontal patients depended on working memory and attentional task demands. Mangels et al. (1998) concluded that the cerebellum functions as a central timing

mechanism that is essential for an accurate representation of temporal information. In contrast, "the pre-frontal cortex subserves supportive functions associated with the acquisition, maintenance, monitoring and organization of temporal representation in working memory" (Mangels et al., 1998, p.15; see also Rubia et al., 1998; Casini & Ivry, 1999).

5.2.2. Basal ganglia

In a recent review, Gibbon et al. (1997) have suggested that the basal ganglia are the key component of an internal pacemaker. Studies involving human subjects with basal ganglia disease have provided evidence for an involvement of the basal ganglia in timing. Artieda et al. (1992) tested temporal discrimination thresholds for recognition of paired sensory stimuli in 44 Parkinson's disease patients. The data revealed a significant increase of temporal discrimination thresholds in these patients. Similarly, Pastor et al. (1992) reported impaired time estimation and reproduction in a group of Parkinson's disease patients. Furthermore, Parkinson patients are more variable on a repetitive tapping task after omission of their normal L-dopa medication (O'Boyle et al., 1996). Similar problems have been reported in patients with Huntington's disease (Freeman et al., 1996).

5.2.3. The neuropharmacology of timing and time perception

Neurotransmitters and certain centrally active drugs are known to have specific effects on timing behaviour (for a review see Meck, 1996). Metamphetamine and neuroleptic drugs like haloperidol and chlorpromazine which interfere with the neurotransmitter dopamine change the clock mechanisms without impairing the memory or decision stage (Meck, 1983). Similarly, upsetting the balance of the serotonin metabolism has been shown to have consequences for the clock speed (Meck & Church, 1987a). Other drugs, like the cholinesterase inhibitor physostigmine and the cholinergic receptor blocker atropine, appear to have an influence on memory storage (Meck & Church, 1987b). In short, the clock system is mainly influenced by the dopamine metabolism while the memory system is largely cholinergically based.

5.3. The time bisection paradigm

5.3.1. Introduction

As far as we are aware, there are only two studies that have applied the time bisection paradigm to assess time perception in patients: Nichelli et al. (1995) examined stroke patients who had suffered damage to the frontal lobe. In a later study, Nichelli and his colleagues tested subjects with cerebellar degeneration (Nichelli et al., 1996). Both studies confirmed the importance of the cerebellum and the frontal lobe in timing.

In our study, the time bisection paradigm has been used for the first time to explore time perception in unilateral neglect patients. More specifically, the objective of this study was to analyse hemispheric differences of duration processing in stroke patients with and without neglect. Unlike in Nichelli et al.'s studies (1995, 1996), only patients were selected whose cerebral damage did *not* include any of the structures known to be involved in timing. The rationale of this technique was that if any distortions in duration processing emerge, the impairment would not have been caused by a specific malfunction of the clock or the memory mechanisms. Figure 3 illustrates a simplified version of the scalar timing model (Nichelli et al., 1996).

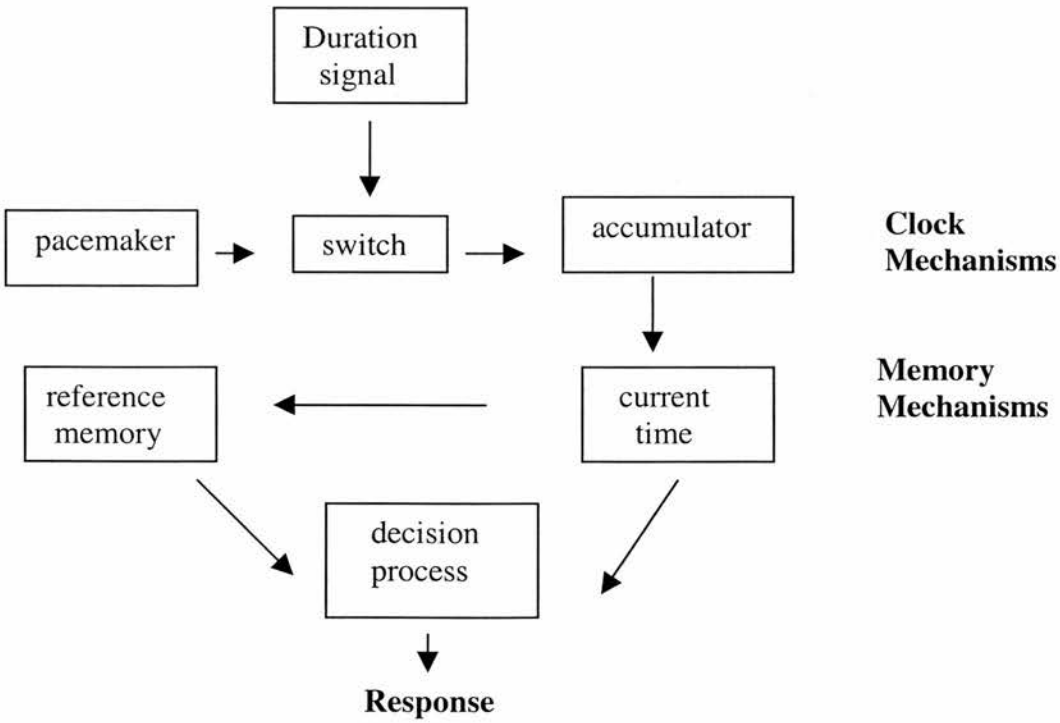

Fig.3: A simplified version of the scalar timing model (Nichelli et al., 1996, p.865).

Based on the evidence presented in the fourth chapter, we have claimed that the damaged hemisphere of the stroke patient is slowed down in its neuronal processing. Thus, we hypothesise that both stroke patient groups will display consistent changes in the perception of time intervals compared to control subjects. However, neglect subjects will demonstrate more pronounced deviations than non-neglect stroke patients. According to the scalar timing model, when the hemisphere is slowed down, fewer pulses are accumulated in the accumulator. That means, a time interval is perceived as passing more quickly than it actually does. In other words, time passes more quickly in the damaged hemisphere.

In summary, the motivation for this experiment was to corroborate our hypotheses that processing in the ipsilesional hemisphere is slower than the processing in the contralesional hemisphere.

5.3.2. Methodology

5.3.2.1. Inclusion/exclusion criteria and the neuropsychological assessment of subjects

5.3.2.1.1. History and lesion site

Only subjects with right-sided deficits were considered for this study to avoid complications caused by aphasic symptoms. Potential speech impairment was discussed with the speech therapist of each patient. Patients with previous trauma to the right hemisphere were not excluded. Further exclusion criteria were a psychiatric history, general neurological pathologies (e.g. epilepsy) and alcohol abuse in the past and present.

Patients with focal lesions of the cerebellum, basal ganglia and pre-frontal cortices were excluded from the experiment as these structures are involved in timing (Meck et al., 1984, 1987; Meck, 1988; Ivry et al., 1988; Olton, 1989; Ivry, 1996; Gibbon et al., 1997). Furthermore, patients with temporal cortex damage were not included as the temporal cortex, particularly the right temporal cortex, has been associated with the retention of a precise analogue representation of auditory tonal patterns (Liégois-Chauvel et al., 1998; Nishitani et al., 1998; Penhune et al., 1999). Also, patients with hippocampal damage were excluded although recent evidence suggests that hippocampal lesions might not impair auditory working memory (Alain et al., 1998).

5.3.2.1.2. Drugs

Patients who were taking the following centrally active drugs were also excluded as these drugs have been shown to alter time perception: Metamphetamine, neuroleptic drugs, antidepressants, cholinesterase inhibitors (physostigmine) and atropine (Meck, 1983; Meck & Church, 1987a,b; Meck, 1996). The clinically most commonly used drugs that fall in this category are antidepressants.

5.3.2.1.3. Unilateral neglect

The criterion whether to include a patient as neglect or control patient was his/her performance in the star cancellation task. Halligan et al. (1989) evaluated the test sensitivity of the most commonly used clinical neuropsychological tests (line crossing, letter cancellation, star cancellation, figure and shape copying, line bisection and representational drawing). Halligan et al. (1989, p.910) concluded that the star cancellation test was "an extremely sensitive measure of neglect" ... "It lends itself to very detailed experimental analysis and is well adapted to rapid accurate diagnosis" (Halligan et al., 1989, p.910). It had a sensitivity of 100% which was better than any of the other tests. Closest to this result came the letter cancellation test with 80% sensitivity. Representational drawing, a popular bed side test, was shown to be sensitive in only 37% of patients that were classified as suffering from neglect according to the aggregate score from all six tests.

Some authors argue for the application of a wide range of different tests. In our study we decided to choose the most sensitive test of all six examined in Halligan et al.'s study (1989) and to repeat it during the course of the experiment twice.

The stimuli in the star cancellation task are 52 large stars, 13 letters, 10 short words and 56 small stars. The patient was asked to cross out all the small stars. Before the test two small central stars were crossed out for the purpose of demonstration by the examiner. The test was presented in mid-sagittal position. The possible score was therefore 54, i.e. 27 on each side. The patient was not allowed to move the stimulus paper. No restrictions were imposed on head and eye movements.

A patient was classified as neglect patient if the score on the left side of the star cancellation test dropped below 20. If the score increased above this cut-off line during repeated testing, the patient was excluded from this patient group. Control

stroke patients, i.e. stroke patients without neglect, were only included when the score on each side of the test was not below 25.

5.3.2.1.4. Hearing

A simple clinical bed side test was used. The examiner said a number increasingly loudly in one ear whilst blocking the other ear with a finger. The patient was asked to repeat the number. If there was evidence for a hearing impairment, the level of loudness of the marker tone was repeatedly changed until the patient indicated hearing the sound clearly. The same level of loudness was maintained throughout the following sessions. This procedure gave only a crude indication of the patient's hearing impairment but the test is part of daily medical practice (Hope et al., 1989). Slight hearing impairment was not regarded as a reason for exclusion. It has been demonstrated that the discrimination of empty intervals was independent of the intensity of the auditory marker sound that marked the interval to be assessed (Allan, 1979).

One of the caveats in presenting marker sounds to stroke patients is that an effect could be due to an impairment on a perceptual level. However, Bisiach et al. (1984) who reviewed the relevant literature did not find support for this possibility that unilateral lesions lead to a contralesional hearing loss. Absolute thresholds are not impaired after one-sided damage according to the orthodox view (Jackson, 1876, see Jackson, 1931), a position that has found support in more recent studies (for a review see Neff et al., 1975).

Gersuni (1965) and Karasseva (1972) presented evidence that damage to the temporal lobe may affect the perception of sounds of a few millisecond duration when presented to the contralesional ear. Also, Karp et al. (1969) reported an increased threshold of the contralesional ear in 10 out of 19 right hemisphere subjects. Supporting the classical view, Ruff et al. (1982) tested patients who mislocalised sounds and who suffered lesions to right posterior brain areas. No impairment was found in pure tone thresholds. Similarly, Bisiach et al. (1984) did not report any significant contralesional deficit in pure tone audiometry. However, even if there is a slight hearing impairment discovered in the bed side test, the volume of the marker sounds can be set at a slightly higher level than for subjects

with normal hearing. The discrimination of empty intervals, as they are used in this study, is independent of the intensity values of the auditory signals that bind the interval to be judged (Allan, 1979).

5.3.2.1.5. Auditory working memory

We decided to test the patients' prosody and auditory working memory as the closest approximation to a measure of the working memory for temporal patterns. Patel et al. (1998) explored the relationship between the processing of melodic and rhythmic patterns in speech and music and concluded that the processes involved to maintain auditory patterns in working memory overlap. A test of working phonological memory was proposed by Gathercole (1995; see appendix 1). Gathercole (1995) who tested a group of four and five year olds designed two lists of 20 'low' word-like non-words (e.g. 'underbrantuand') and 20 'high' word-like non-words (e.g. 'sladding'), respectively, containing 2, 3, 4, and 5 syllables. It was demonstrated that the repetition of low word-like stimuli reflected the function of phonological working memory.

The same technique as used by Gathercole (1995) was adopted in this study. The patient was told at the beginning of the test that they would hear some "funny sounding words" and was ask to repeat the word and to copy intonation and pitch of the word immediately. The experimenter sat behind the patient so that lip-reading was excluded. The patient had 3 s to repeat the word and then was encouraged to make an attempt. If the patient's repetition was regarded as accurate, the attempt was scored 1. If the experimenter considered the response as inaccurate, it was scored 0. The total score was therefore 20. If the score was below 17 the patient was not included in the study.

5.3.2.1.6. Long-term memory

A word repetition test was conducted. 10 words controlled for frequency were selected from the CELEX database (CELEX lemma frequency; frequency out of 17.9 million words) (see appendix 2). The words were read out twice to the patient at the beginning of the training session. He/she was told to memorise the words because the experimenter would ask for them after the session. After the first session which

lasted 20 min the experimenter asked for the reproduction of the words. The possible score was 1 for each word, so the total to be achieved was 10. Patients with a score of below 4 where excluded from the study.

5.3.2.2. Subjects

Patients from the stroke rehabilitation unit from Drumchapel Hospital, Glasgow, participated in our study. Two neglect (two female patients, mean age 78 years) and two non-neglect stroke patients (two male patients, mean age 66 years) were examined[2]. The patients had suffered either acute or chronic right hemisphere injury as demonstrated by CT- or MRI-scan without any record of previous cerebral injury. Two healthy subjects were examined as a control group (one female, one male subject, mean age, 70.5 years). There was no previous illness in the past medical history of the control group (see tables 2, 3 for subjects' profile). The age difference between the three groups was not significant. All subjects fulfilled the criteria set for auditory acuity and memory function.

Table 2: Profile of patients and control subjects in study.

Subject/age/handedness/sex	**CT/MRI-lesion**	**Time from cerebral injury at time of testing**
Neglect Patients:		
1/82/R/F	R parietal infarct	41 weeks
2/74/R/F	R parietal infarct	3 weeks
Non-neglect Patients:		
3/72/R/M	R parietal infarct	3 weeks
4/60/R/M	R posterior limb of internal capsule	6 weeks
Control Subjects:		
5/78/R/F	-	-
6/63/R/M	-	-

[2] Formal ethical approval had been obtained from the West Ethics Committee, Glasgow.

Table 3: Patients' and control subjects' performance on star cancellation task, phonological working memory and long term memory.

	Star cancellation tests 1 Side and number of stars cancelled	2	3	Auditory working memory score	Long term memory score
Neglect Pts.					
1	R/27 L/16	R/27 L/17	R/27 L/13	18	5
2	R/7 L/0	R/11 L/0	R/27 L/12	17	5
Non-Neglect Pts.					
3	R/27 L/27	R/27 L/27	R/27 L/27	18	6
4	R/27 L/27	R/27 L/27	R/27 L/27	19	5
Control Subjects					
5		Not tested		18	5
6		Not tested		19	6

Note. The scores in the auditory working memory and long term memory tests refer to the number of correct responses.

5.3.2.3. Apparatus

An apple MacIntosh computer LC 475 controlled all experimental events. It was stationed in one of the hospital rooms. All the experiments were conducted in this room and its interior never changed. Only patient no. 1 was visited at home and the experiment was performed in the same room at the same time of the day.

The temporal stimuli were formed by two identical 30 ms rectangular sounds (2000 Hz) marking an empty interval of different durations. 2000 Hz was chosen as marker frequency because it falls comfortably into the frequency range of the normal ear which is 16 to 16 000 Hz (Habermann, 1986).

All visual displays were presented on a standard 15 inch black-and-white computer monitor. A button box was used and two of its buttons were labelled SHORT and LONG. The buttons were operated by the experimenter after the patient had given an oral response. Presses on these two buttons represented the classification response. The button box was out of the patient's sight. The program with which the experiment was written was PsyScope 1.1. A closed set of ear phones was used (Sony, MDR CD 550).

5.3.2.4. Design

A mixed design was used. The between subject variable was cerebral damage with three levels (no cerebral damage, damage with unilateral neglect and cerebral damage without neglect). Two dependent variables were measured: The position of the curve which represented the subjects' responses, which is referred to as the bisection point, and the subjects' ability to discriminate the test stimulus, the Weber fraction (see below for further explanation). The independent within variables were the duration of the test time intervals with 10 levels (ranging from 700 to 3300 ms) and the hemisphere to which the test rhythm was presented (2 levels, left and right hemisphere). All subjects were presented with the same stimuli for all conditions.

5.3.2.5. Stimulus material and procedure

The short standard interval had a duration of 500 ms and the long standard interval had a duration of 3500 ms[3]. The test intervals were of varying durations (700, 1000, 1300, 1600, 1900, 2100, 2400, 2700, 3000, 3300 ms). The beginning and end of each interval was marked by a 30 ms rectangular sound of 2000 Hz.

The experiment began with five presentations of the standard short (500 ms) and standard long (3500 ms) time interval stimuli which were presented to one ear through a set of closed ear phones (see app. 8a for the instructions to the subjects). The two standard intervals were only presented to this one ear. The standard intervals were identified before delivery by an appropriate display ("SHORT" which was placed to the right of a central cross. The cross was meant to function as a cue to facilitate the perception of the instruction). Following the display there was a delay of 500 ms, then the standard interval marked by two 30 ms sounds was presented. The end of this presentation was indicated by the word "END" (again placed to the right of a central cross). There was an inter-trial interval of 1.5 s. Then the next standard interval was presented. This was repeated five times. The order of the standard stimuli was randomised.

[3] The time bisection paradigm reported in the present study has to be classified as a category rating task as the ratio between the long and the short standard is greater than 4. However, a time bisection experiment is classified as a discrimination task whenever the long/short ratio does not exceed 2 (see table 1).

Then subjects received a trial sequence of the ten different test durations. During this session, test intervals were only presented to the other ear which was different from the ear to which the standard intervals were played. The beginning of the test stimulus was marked by the word "TRIAL" which was placed to the right of a central cross. After a delay of 500 ms the test interval was presented, again marked by two sounds of 30 ms duration. The end of the test interval was marked by the word "END" which was displayed 500 ms after the second sound. During each trial interval, the patient was instructed to repeat the word "GO" to prevent chronometric counting.

After the response "SHORT" or "LONG" was given by the subject, the experimenter pressed the appropriate button of the button box. The press of the button then delivered the next test interval without delay. The inter-trial interval varied up 5 s. When the subject did not respond, the experimenter would try to prompt the subject by saying "WHAT IS YOUR RESPONSE?", for example. Each trial sequence consisted of the ten stimuli presented in random order. Each trial sequence except the last was followed by two presentations of the standard short and standard long stimuli, arranged as at the start of the experiment. Standard and test intervals were never presented to the same ear.

During one session subjects received one, two or three different trial sequences to each ear depending on the clinical condition, thus performing two, four or six classifications of each of the ten trial stimuli. The subjects were instructed to classify each trial stimulus on the basis of its perceived similarity to the standard short and standard long intervals. The side of presentation was varied from session to session, i.e. if the first trial sequence was presented to the left ear in session one, in session two the trial sequence would be presented to the right ear etc.

As practice, before the start of the experiment proper, each subject received an initial five presentations of each of the standard stimuli to both ears and the first trial sequence of ten test intervals to both ears. The experiment was then restarted from the beginning and ran as described above. After ten, 20 or 30 classifications depending on the clinical condition, the experiment was restarted and ran as described above. This time the presentation of the standard and test stimuli were reversed and presented to the other ear. Subjects took about 20 minutes to complete

the experimental session. In total, subjects completed six to twelve sessions. In total, 18 classifications for each stimulus duration were made.

5.3.2.6. Results

A probit analysis was performed that produced a transformed plot of the data. The probit transformed plot allowed the calculation of the 'bisection point' which was defined as the test time interval which was classified as "long" on 50% of the trials. The difference limen was obtained which was half the difference of the test rhythm classified as "long" on 75% of trials and that classified as "long" on 25% of the trials. The Weber Fraction was calculated by dividing the difference limen by the bisection point (figure 4). The Weber Fraction represents a measure of the subjects' accuracy, i.e. of their ability to discriminate that specific kind of stimuli. An ogive curve was obtained for each ear condition covering the range of the test intervals from 700 ms to 3300 ms duration.

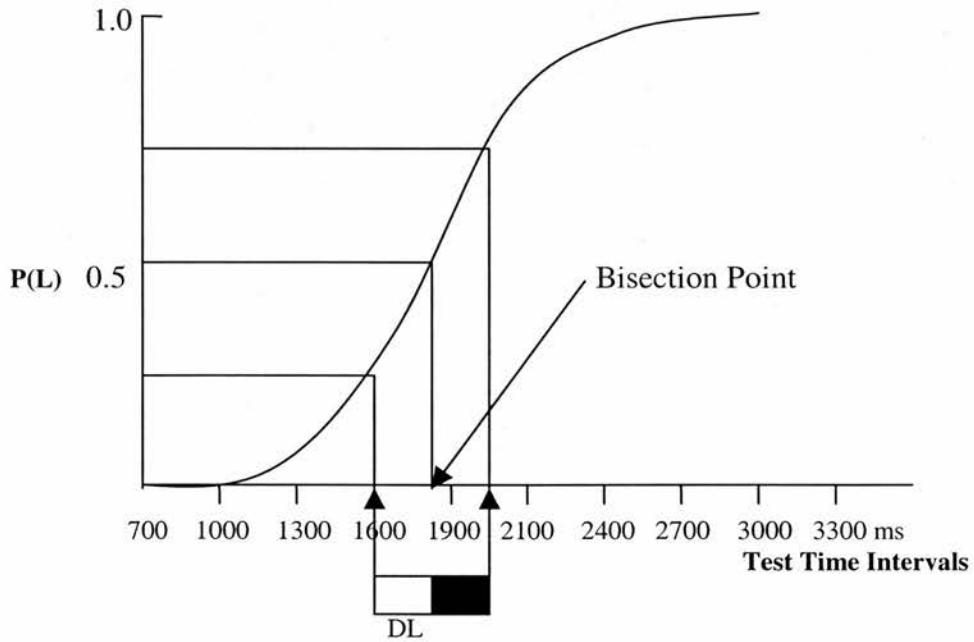

Fig. 4: Example for probit transformed plot of the interval bisection task covering test time intervals from 700 to 3300 ms. The arrow points to the bisection point. The difference limen (DL in the figure) is half the difference between the test rhythm classified as "long" 75% and 25% of the times (i.e. half the difference between values on the abscissa corresponding to probability P(L) = 0.75 and to P(L) = 0.25). As a consequence of Weber's Law, to obtain a measure of the subject's ability to discriminate test rhythms, the difference limen has to be weighted based on the individual's bisection point. The Weber Fraction is defined as "difference limen"/"bisection point".

To summarise our predictions (table 4): The motivation of this experiment is to demonstrate slowed down processing in the damaged hemisphere. More precisely, we want to show that time passes more quickly in the injured side of the brain than in the intact hemisphere. We hypothesise that the effect will be significantly stronger in the neglect group compared with the non-neglect stroke group. According to scalar timing theory, time passes more quickly in the damaged hemisphere because fewer pulses are accumulated in the accumulator. When the reference intervals are presented to the left ear, i.e. the right damaged hemisphere, the reference intervals will be perceived as shorter than they are because relatively fewer pulses are counted over a unit of time. Consequently, the bisection point of the test intervals presented to the intact hemisphere where relatively more pulses are counted will shift to the left, to shorter time intervals. Conversely, when the reference intervals are played to the intact hemisphere, relatively more pulses are counted compared to the damaged hemisphere. The test intervals are perceived as shorter than they are in the damaged hemisphere (relatively fewer pulses are counted). Therefore, relatively longer test intervals compared to the reference intervals will be judged as 'long' and the bisection point moves to the right, i.e. towards longer intervals.

Table 4: Predictions on bisection point shift.

Reference Interval	Test Interval	Bisection Point Shift
Left ear/RH	Right ear/LH	Left shift
Right ear/LH	Left ear/RH	Right shift

Unfortunately, the neglect patients' performance in judging the test intervals was so erratic that the probit analysis did not produce a meaningful bisection point (see figures 5a,b). Therefore, the bisection point data of the neglect group had to be excluded from the statistical calculations.

Position of bisection point

After presentation of the reference time intervals to the left ear, the mean position of the bisection point was at 1770 ms for the non-neglect group and at 1609 ms for the control group. When the reference time intervals were presented to the right ear, the

position of the mean bisection point was at 1891 ms for the non-neglect group and at 1658.5 ms for the control group (table 5).

Table 5: Mean bisection points for non-neglect and control groups. Test time intervals range from 700 to 3300 ms.

	Reference intervals L ear	Reference intervals R ear
Non-Neglect Group	1770 ms	1891 ms
Control Group	1609 ms	1658.5 ms

Two non-parametric Kruskal Wallis tests were performed which did not reveal any significant differences of the bisection point between the non-neglect and the control group in either ear condition (reference intervals to left, $\chi^2 = 1$, $d.f. = 1$, $p > 0.05$, and right ear, $\chi^2 = 1$, $d.f. = 1$, $p > 0.05$).

Comparing the bisection point between the two ear conditions, the position of the bisection point in the control group shifted to the right by 49.5 ms after the reference intervals were presented to the right ear. The shift was not significant (non-parametric Friedman test, $\chi^2 = 0.3$, $d.f. = 1$, $p > 0.05$). In the non-neglect group, the bisection point shifted, as predicted, to the right by 121 ms in the right ear condition. The right-shift in the non-neglect group was not significant either (Friedman test, $\chi^2 = 1$, $d.f. = 1$, $p > 0.05$).

In summary, there was no difference of the bisection point position between the non-neglect stroke (NN group) and the control group (C group). Furthermore, both in the control and the non-neglect group, there was a shift to the right when the reference intervals were presented to the intact hemisphere and the test intervals to the damaged hemisphere. The graphs below represent the performance of each group including the neglect patients (N group) for each presentation condition (figures 5, 6 and 7 a, b).

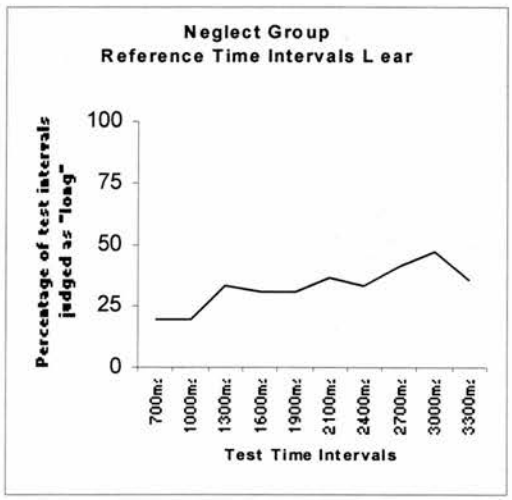

Fig. 5a: Neglect Group. Left ear condition.

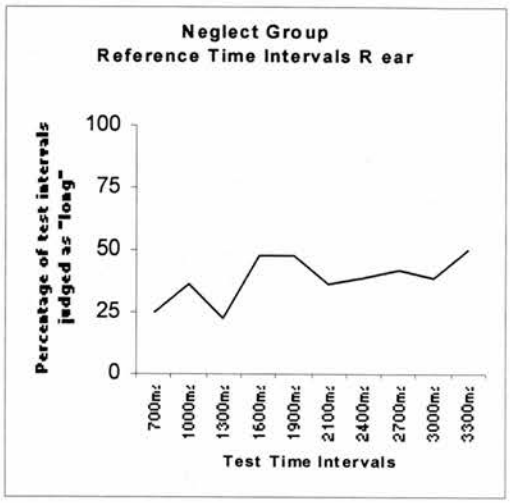

Fig. 5b: Neglect Group. Right ear condition.

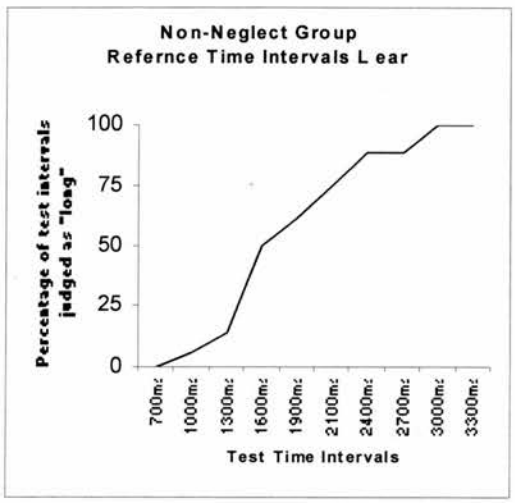

Fig. 6a: Non-Neglect Group. Left ear condition.

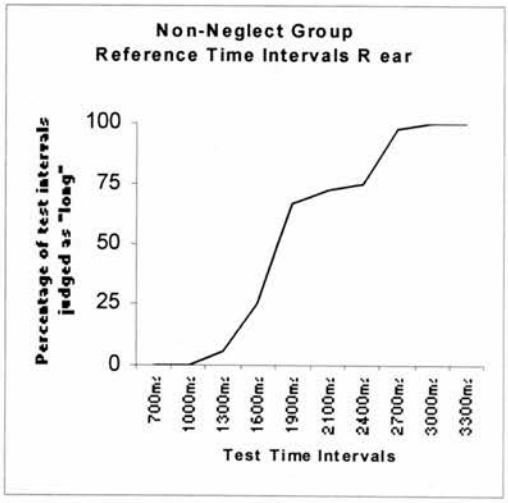

Fig. 6b: Non-Neglect Group. Right ear condition.

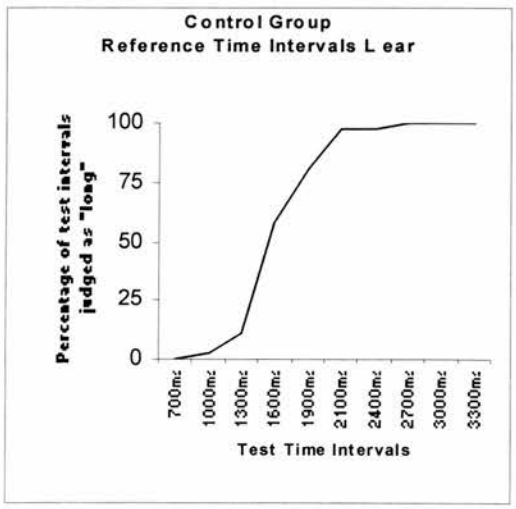

Fig. 7a: Control Group. Left ear condition .

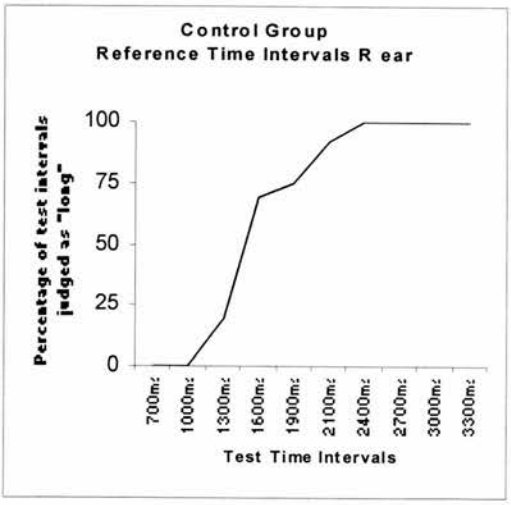

Fig. 7b: Control Group. Right ear condition.

Weber Fraction

The Weber Fraction represents a measure of the subject's ability to discriminate this specific kind of stimulus. When the reference time intervals were presented to the left ear, the mean Weber Fraction was 0.73 for the neglect group, 0.12 for the non-neglect group and 0.12 for the control group (table 6). After presentation of the reference time intervals to the right ear, the mean Weber Fraction was 0.8 for the neglect group, 0.11 for the non-neglect group and 0.12 for the control group (table 6).

Table 6: Mean Weber Fraction for neglect, non-neglect and control groups; test interval range 700 to 3300ms.

	Reference intervals L ear	Reference intervals R ear
Neglect Group	0.73	0.8
Non-Neglect Group	0.12	0.11
Control Group	0.12	0.12

Two non-parametric Jonkheere tests for ordered alternatives were performed to compare the performance of the three groups for the left and right ear condition. Both tests yielded the same non-significant result (C < NN < N; $J = 10$, $p > 0.05$). The Weber Fractions for the non-neglect and the control group were almost identical whereas the Weber Fractions of the neglect groups was greater for both the left and right ear conditions. However, the difference only approached significance levels between the neglect group and the non-neglect group (Kruskal Wallis test, reference intervals to left ear, $\chi^2 = 2.6$, $d.f. = 1$, $p = 0.1$, and right ear, $\chi^2 = 2.4$, $d.f. = 1$, $p = 0.1$) and between the neglect group and the control group (Kruskal Wallis test, reference intervals to left ear, $\chi^2 = 2.4$, $d.f. = 1$, $p = 0.1$, and right ear, $\chi^2 = 2.4$, $d.f. = 1$, $p = 0.1$).

When comparing the discrimination of the test intervals between the left and right ear condition, there were no significant differences in any group (neglect group: Friedman test, $\chi^2 = 2$, $d.f. = 1$, $p > 0.05$; non-neglect group, $\chi^2 = 1$, $d.f. = 1$, $p > 0.05$; control group, $\chi^2 = 1$, $d.f. = 1$, $p > 0.05$)

In summary, the non-neglect group was as good as the control group as discriminating the test intervals whereas the neglect patients displayed a deficit in the discrimination of the stimuli with the difference being marginally significant.

Furthermore, the accuracy of the subjects' performance was independent of the side to which the standard and test intervals were presented.

5.3.2.7. Discussion

In this study we tested duration processing of stroke patients with and without neglect and of normal control subjects in the time bisection paradigm. The obtained results fit our predictions: Non-neglect stroke patients displayed a rightward shift of the bisection point after presentation of the reference intervals to the right ear. The obtained shift, albeit not significant, is compatible the claim that the damaged hemisphere is slowed down in its processing capacity. There was also a slight non-significant rightward shift of the control group. However, the shift of the non-neglect group was one and a half times greater.

The ability to represent temporal information requires attentional and memory processes. The performance of the neglect patients was so erratic to the extent that the bisection point could not be used for analysis (see fig. 5a, b). We have to conclude that the task demands imposed by the time bisection paradigm exhausted the processing capacities of the neglect patients. The failure of the neglect patients to discriminate the stimulus intervals is reflected by a Weber Fraction which is greater than that of the non-neglect and control group, with the difference being marginally significant. Nichelli et al. (1995) tested frontal lobe patients in the time bisection interval. Although the frontal lobe has been implicated in timing processes, the patients' data could still be fitted by a logistic regression unlike the data of our neglect group. Furthermore, the Weber Fraction was not significantly worse than the ones of the normal control group in Nichelli et al.'s study (1995). Therefore, our neglect patients must have been considerably more impaired despite intact frontal lobes. We hypothesise that this comprehensive impairment of the neglect group was caused by intra- and interhemispheric desynchronisation. That is, although the structures involved in memory and attentional processes have been spared, their functional integrity was reduced due to a lack of informational binding.

The increase of the Weber Fraction in our neglect population replicates the data of Marshall and Halligan (1989). In a single case study, a patient with left neglect was

examined in a line bisection task. Marshall and Halligan (1989) reported a dramatic increase of the Weber Fraction in the patient's bisection performance.

Basso et al. (1996) presented a single case study of a unilateral neglect patient who displayed some counterintuitive spatial distortions of duration estimation. Target stimuli were displayed in the ipsilesional hemispace due to a hemianopia. The stimulus was a black dot appearing in the centre of a red circle for either 300 ms or 700 ms. The dot was presented in a pseudo-random order in either a left or the right circle (both within the right visual field). After the patient had familiarised himself with the duration of the short and long stimuli during the training phase, he was asked to judge test stimuli of either 300 ms or 700 ms as short or long. The analysis of the data showed that the patient consistently perceived the stimuli in the left-relative position as being longer than they were, i.e. he classified the short 300 ms stimuli as long. Basso et al. (1996) concluded that according to the framework of scalar timing, more pulses were accumulated in the accumulator when a stimulus appeared in the left-relative position. The duration of the stimulus was consequently judged as longer.

These findings are at first sight not reconcilable both with the predictions made by attentional models of time perception and our temporal diplopia theory: First, the attentional interference effect describes the phenomenon that normal subjects shorten the perceived duration when attention is spread across the processing load. The more attention is allocated to non-temporal information, the shorter the perceived duration of the time interval (Brown, 1997). Consequently, as neglect patients allocate less information to left-relative stimuli (Làdavas et al., 1990), the patients should perceive the duration of left-relative stimuli as shorter. The opposite effect was found in Basso et al.'s study (1996). Second, our temporal diplopia theory claims slowing down of neuronal processing. That is, the pulse count in the accumulator should be *de*creased not *in*creased as Basso and his colleagues (1996) have suggested. However, there is an alternative explanation: If we assume that the representation of the long interval in the reference memory buffer (fig. 3) has decayed (the number of pulses have decreased), the patient would perceive the short stimulus duration as long. In other words, the problem might lie in the reference memory not in the

increase of pulses in the accumulator. Continuing this line of argument, we have to account for the spatial differences in the decay of reference memory: An attentional gradient has been postulated by many researchers (Rizzolatti et al., 1985; Kinsbourne, 1987, 1993; Pouget & Sejnowski, 1995, 1996) and attention and memory are inextricably linked. Therefore, we hypothesise that there is a memory gradient linked up with an attentional gradient. A memory gradient can account for the overestimation of stimulus durations in the left-relative position that was reported by Basso et al. (1996). This analysis offers a more parsimonious explanation than an increase of pulses in the accumulator for which there is no neurophysiological evidence.

Finally, a small caveat has to be addressed with regards to the observed rightward shift in the non-neglect group of the current study. If one were to claim impaired attentional processing in the damaged hemisphere of the non-neglect stroke patients, we would expect what we have found: A rightward shift after presentation of the reference intervals to the right ear, because the test intervals are perceived shorter in the damaged hemisphere. However, this explanation is unlikely as the Weber Fraction of the non-neglect group was even minimally better than the one of the normal control group when the reference interval was played to the left hemisphere and the same after presentation of the reference interval to the right hemisphere. Therefore, the rightward shift could be interpreted as a genuine effect reflecting slowed down processing in the damaged hemisphere.

5.3.2.8. Conclusion

For the first time we report a study that examined duration processing of neglect patients in the time bisection paradigm. The results demonstrated that the attentional and memory demands of the experiment went beyond the neglect patients' processing capacity. These findings have to borne in mind for future studies exploring time perception in neglect patients.

However, the results obtained from the non-neglect stroke group fitted the hypotheses made by the temporal diplopia theory. The non-neglect patients displayed consistent changes of time perception predicted by our model. The results are

compatible with the claim that neuronal processing is slowed down in the damaged hemisphere. Interference from attentional and memory deficits have been excluded.

Chapter Six

Rhythm perception in unilateral neglect

In this chapter, we will investigate rhythm perception in unilateral neglect. Recently, Griffiths et al. (1997) has presented a single case study of a neglect patient that explored temporal auditory deficits. In our study, we have designed a paradigm that extends Griffiths et al.'s approach (1997) and introduces novel methodology into the field. More specifically, the experiment explores our claim that in stroke and neglect patients the damaged hemisphere is functioning more slowly than the intact hemisphere. Before the description of the experiment, an introduction to rhythm perception will be presented.

1. Introduction

Rhythm is a fundamental component of music in every culture, but the way auditory temporal patterns are encoded in the brain is far from clear. Neuropsychological investigations of rhythm are generally divided into studies which have examined basic parameters of temporal perception such as perception of duration (Divenyi & Robinson, 1989; Robin et al., 1990; Griffiths et al., 1997; Penhune et al., 1999) and those studies that have focused on the perception of musical rhythms (Peretz, 1990; Platel et al., 1997). In this chapter, we will refer mainly to the former group of studies as our experiment explores the perception of rhythms that are constructed of a simple sequences of identical sounds (equitone) with fixed interstimulus intervals (isochronous).

2. The perception of simple rhythms and their representation: Two theories

2.1. Introduction

Two classes of theories analysing rhythm perception will be presented: First, a theory originally suggested by Schulze (1978) and a related model developed by (Povel

& Essens, 1985); second, the approach which has been taken by Keele et al. (1989), Ivry and Hazeltine (1995) and Ivry (1996).

The constituents of a tonal sequence have two characteristics. They can vary in pitch, loudness, timbre and duration. Furthermore, the onsets of the tones form points in time and thereby divide the time continuum into a sequence of intertone intervals. In other words, the sounds are structures *in time* and generate structures *of time*. Also, there are two processes involved in the perception of a tone sequence: One concerns the characteristic structure of each individual tone, the other the temporal structure of the sequence. Rhythm perception seems to be associated more with the latter than the former (Povel, 1984). In our study only equitone stimuli were used, i.e. stimuli that were identical in their characteristics: Frequency, intensity, spectral composition and duration. Therefore, the object of the research was the processing of rhythm and not the encoding of the structural aspects of the stimuli. Two theories will be presented that deal with the processing and representation of simple tone sequences: The beat-based and interval-based approach to rhythm perception.

2.2. Beat-based processing of simple tonal sequences

Povel and Essens (1985) developed a theory which assumes beat-based processes in rhythm perception. The basic concept of beat-based processing is that an initial sequence of periodic stimuli generates an internal beat which continues after the initial stimulation.

A timer is specified by Povel and Essens (1985) as a hierarchical clock with "equally spaced pulsing" (Povel & Essens, 1985, p.414) which determines the units or the beat of the internal clock. The unit itself is flexible depending on which series of time intervals are analysed. The concept of the internal clock replaced an earlier notion of a "temporal grid" (Povel, 1984) which is basically the same concept. "The temporal grid is a time scale on which the tone sequence is mapped as a first step in the specification of the temporal structure of the sequence. The temporal grid consists of a sequence of isochronous intervals ... and the temporal grid is not a fixed but a flexible structure" (Povel, 1984, p.320).

For example, a series of five isochronous sounds as illustrated below (figure 1a) can have the following possible temporal grid/internal clock units (figure 1b). The

interval between the onsets of two tones in 700 ms, apart from the onsets between the fifth and the following first tone where it is 1400 ms.

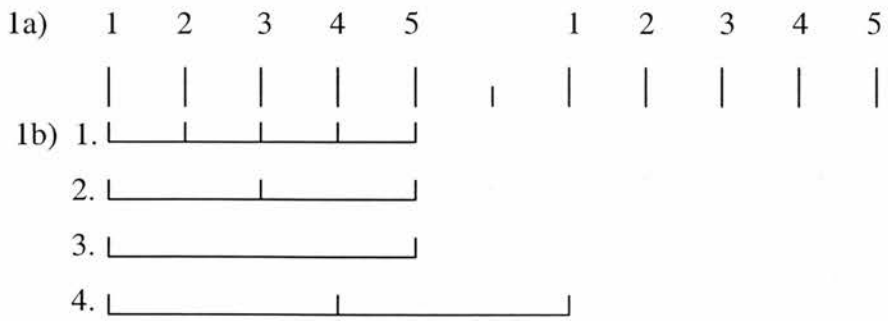

Fig. 1a: A series of single tones. One period contains five tones.
1b: Examples of sequences with their alternative temporal grid/internal clocks units.

The criteria for the selection of a unit follows an economy principle which is defined by Povel (1984, p.320) as follows:

1. " A grid is more economical the more elements it fixates.
2. A grid is less economical the more points in time it fixates at which no tones occur.
3. A grid is more economical the easier the non-fixated elements can be specified within the given grid".

According to these definitions the above series of equitone, isochronous tones (fig. 1a) can be analysed in the following way: Grid 4 is a special example because it exceeds the span of one period. For this reason it is not a practical grid. Grid 3 which stretches over the entire period is discarded as very uneconomical because it only fixates two elements. Since we are analysing an isochronous tone sequence the second economy criterion does not apply: There are no points in time at which no tones occur. Applying the two economy criteria, grid 1 appears the most economical out of the remaining two grids because it fixates all elements, i.e. there are no non-fixated elements that have to be specified. Unlike grid 2, where only the first, third and the fifth element are fixated. Element 2 and 4 could be specified by saying that the two intervals of the grid can be subdivided into two equally long intervals. This is clearly a less economical description compared to grid 1.

In sum, a sequence of isochronous tones can be encoded economically. This means that the given temporal pattern will be reproduced more easily or judged as less complex compared to temporal patterns where either no internal clock has been induced (where no matching temporal grid has been generated) or where the encoding of the sequence is relatively complex (Povel & Essens, 1985).

In an earlier paper, Schulze (1978) had advocated a beat-based analysis of regular rhythmic patterns compared to an interval-based approach. In this study, Schulze (1978) presented the subjects with a sequence of seven or nine tones forming a succession of six or eight intervals (only the former is represented in fig.2a-d). The subject was asked to judge whether the intertone intervals were all identical to each other or differed. The control sequence was a series of tones with an intertone interval T of 300 ms which can be represented as follows:

Fig. 2a) T T T T T T

In the first condition the first two intervals were unchanged but the following intervals were all increased by10 ms as (2b) illustrates:

2b) T T T+ T+ T+ T+

In condition 2, only the third interval was increased with the following intervals being 300 ms long.

2c) T T T+ T T T

In the final condition, the third interval was increased and the fourth interval decreased by the same increment which will yield the following representation:

2d) T T T+ T- T T

From this set up, different predictions arise depending on the underlying processing mechanism of the tone sequences. If a beat-based approach is used, condition (2b) should be the easiest followed by condition (2c) and then (2d). The prediction is based on the fundamental assumption that the first three tones start an internal beat that persists during the following tone sequence. The subsequent tones do not alter the beat once it has been established. Condition (2b) is easiest because the internal beat will be out of synch with the fourth beat by 10 ms, with the fifth beat by 20 ms, with the sixth by 30 ms and with the last beat by 40 ms. Condition (2c) is more difficult than (2b) but easier than (2c) because the first incremented interval will

produce an asynchrony of 10 ms. Since the remaining intervals drop back to normal, the asynchrony initiated with the single increment will maintain itself at 10 ms for all remaining beats. In other words, this condition creates four beats that are out of synch with the internal beat by 10 ms. Condition (2c) on the other hand is the most difficult because while the fourth beat produces an asynchrony with the internal beat, the fifth beat restores synchrony.

Schulze (1978) also investigated an interval-based process of analysis. The predictions differ from the beat-based approach as will be explained in the following section.

2.3. Interval-based processing of simple tonal sequences

Schulze (1978) proposed two versions of the interval timer. In the first one, termed the adjacency model by Keele et al. (1989), adjacent intervals within the tone sequence are judged. Within this model, condition (2d) of the above described experiment from Schulze (1978) should be the easiest to analyse because three pairs of adjacent intervals differ in duration, whereas in condition (2c) there are only two pairs and in condition (2b) only one.

The second version of the interval-based theory is the memory model. According to this theory, the average duration of the first two intervals is stored in a memory buffer. Subsequent intervals are compared to this average duration. The predictions for the experiment are that condition (2b) is the easiest followed by conditions (2d) and (2c). Condition (2b) should be the easiest task because there are four comparison intervals that differ from the memory trace, whereas in condition (2d) there are two and in condition (2c) there is only one (Keele, 1989).

In the final analysis of the results, Schulze (1978) found support for the beat theory. Keele et al. (1989) repeated Schulze's paradigm and arrived at a different conclusion. The interpretation of their results (Keele et al., 1989) favoured an interval-based process. In an attempt to reconcile the differing results, Keele et al. (1989) proposed that Schulze's subjects preferred a non-obligatory beat-based approach in the analysis of the rhythms. Or alternatively, the interval timer might operate in a beat mode if the timed interval is recycled continuously from start to end.

Keele et al. (1989) summed up the most fundamental characteristics of the discussed timing mechanisms in the following words: The beat-based timer "refers to a time keeper similar to a metronome in which initial events set up an internal rhythm that serves as a benchmark against which to judge other events. In contrast, a memory interval timer can measure intervals that start at arbitrary times, rather than being synchronised with the hypothetical internal rhythm. This mechanism is analogous to a stopwatch. Put another way, a beat-based timer involves comparisons of the time of events. An interval timer involves comparisons of the durations of intervals" (Keele et al., 1989, p.252).

3. Particularities in the perception of isochronous equitone sequences

In the last chapter, we discussed the methodological problems of time perception which apply also to rhythm perception. Beyond that, there are the following particularities specific to the perception of isochronous equitone rhythms which are used in the current study.

3.1. Grouping

When a subject listens to a sequence of equitone sounds which are spaced at equal intervals, a grouping phenomenon might emerge. Grouping is a variable phenomenon which is not very stable or might not be present at all. This perceptual phenomenon can also be described as a "subjective rhythm" (Povel, 1984, p.318) and characterises the fact that a subject might spontaneously group isochronous equitone sounds into sets of 2, 3 or 4 beats. There seems to be a particularly strong tendency to organise a sequence of sounds into a group of four beats (Bolton, 1894; quoted by Povel, 1984). The speed of the rhythms seems to have an influence on this effect, too. The faster the rhythm the more sounds appear to be allocated to one group (Povel, 1984). However, it does not appear that the phenomenon of grouping has an influence on the perceived tempo of the rhythm.

3.2. Gap principle

The gap principle describes the phenomenon that the longest interval within a sequence of sounds marks the end of the perceived pattern. If we applied this

principle to the sequence in fig.1a, which is typical of the rhythmical structure used in the current study, the first beat of the second cycle will be stressed. This rhythmical emphasis might have an affect on how the whole second sequence is grouped but not on the basic temporal grid unit because the temporal unit is based on the beat intervals of the first rhythm according to the beat-based model of rhythm perception (Povel, 1984). Whether the beats of the second rhythm will be perceived as occurring at the same time intervals as the beats of the first rhythm or not, will depend on the position of the beats in the second rhythm with regard to the basic temporal grid.

3.3. Tempo

The tempo of a beat sequence has two effects on the perception of rhythms: First, whether it is perceived as a rhythm at all and, second, which temporal grid is chosen. A sound sequence is only perceived as coherent when it is presented at intervals ranging from 125 ms and approximately 1500 ms. If the onset interval is shorter than 125 ms, the sound sequence is perceived as "an inarticulated train of events" (Povel, 1984, p.330). On the other hand, when the intervals exceed approximately 1500 ms the events will not be perceived as belonging together.

Also, within these boundaries, there seems to be a general rule that the faster the tempo of the rhythm, the more events will subdivide one temporal grid unit. For example, if the smallest interval is 400 ms (figure 3a) or more, subjects beat according to grid (3b). If the tempo speeds up, the grid in (3c) will be chosen (Povel, 1984).

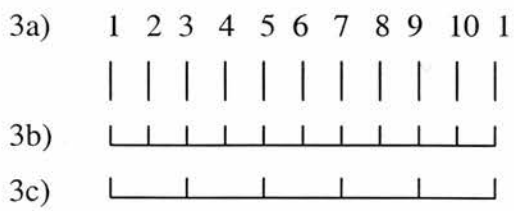

Fig. 3a) A sequence of equitone, isochronous beats.
3b) Grid if intertone interval in (3a) approximates 400 ms.
3c) Grid if intertone interval in (3a) is smaller than 400 ms.

The next section will introduce a rhythm perception paradigm developed to investigate our claim that time passes more quickly in the damaged hemisphere. Or in other words, rhythms are perceived as passing more quickly than they are.

4. The rhythm perception paradigm

4.1. Introduction

Most studies that have investigated impaired rhythm perception in brain damaged patients have been motivated by the aim of identifying neuroanatomical structures that are involved in normal rhythm processing (Mavlov, 1980; Peretz, 1990; Robin et al., 1990; Griffiths et al., 1997; Penhune et al., 1999). However, the purpose of the experiment presented in this chapter is to analyse hemispheric differences of rhythm perception in stroke patients with and without neglect. We selected only patients in whom the neuroanatomical areas known to mediate rhythm perception had been *spared* by the cerebral lesion.

Based on our temporal diplopia theory presented in the fourth chapter, we hypothesised that both patient groups will display consistent changes in the perception of rhythms compared to control subjects. However, neglect subjects will demonstrate more severe deviations than non-neglect stroke subjects. The reasoning is rooted in the scalar timing model outlined in the last chapter (figure 4).

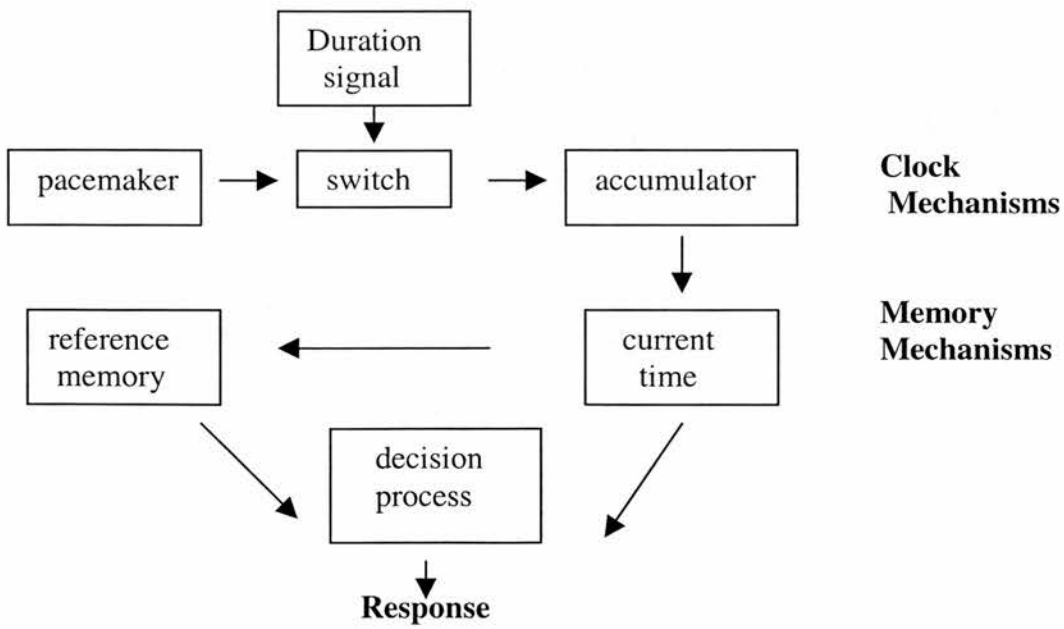

Fig.4: A simplified version of the scalar timing theory (Nichelli et al., 1996).

The experimental paradigm in the current study has been designed as a same/different judgement task: A reference rhythm of fixed speed is presented to one hemisphere. A test rhythm of either the same or different speed is presented to the other hemisphere. The subject is asked to compare the test rhythm with the reference rhythm. It will be argued that the rhythm presented to the damaged hemisphere will be judged as faster than it actually is. We have hypothesised that there is general slowing down of neuronal processing. If this assumption holds true, the rhythm presented to the 'slower' hemisphere will be perceived as faster because, according to the scalar timing model, fewer pulses are accumulated in the accumulator.

The rhythm paradigm[4] was designed in a way that the task was exclusively sensory. Potential deficits in the motor system cannot be excluded in patients who have suffered cerebral trauma even if the movement is executed by the undamaged hemisphere (Day, 1996).

4.2. Methodology

4.2.1. Inclusion/exclusion criteria and the neuropsychological assessment of subjects

The inclusion and exclusion criteria remain the same as described in the time bisection experiment. Patients with lesions to the pre-frontal are excluded because the pre-frontal cortex appears to play a crucial role in auditory working memory (Zatorre et al., 1994; Alain et al., 1998). Furthermore, patients with temporal cortex damage were not included as the temporal cortex, particularly on the right side, has been associated with the retention of a precise analogue representation of auditory tonal patterns (Liégeois-Chauvel et al., 1998; Nishitani et al., 1998; Penhune et al., 1999). Care was taken to exclude patients with hippocampal damage although recent evidence suggests that hippocampal lesions might not impair auditory working memory (Alain et al., 1998).

The long term memory test was not performed as only auditory working memory processes were involved in the task. Figure 5 illustrates the set up of the test sequences used in the paradigm described below. When a subject compares the fourth interval of the standard rhythm (A) with the first interval of the test rhythm

[4] The experiment has been developed in collaboration with Dina Kronhaus, an MSc-students in the department of the Centre of Cognitive Science, University of Edinburgh.

(B), only 3000 ms at the most will have passed – a time interval that lies within the boundaries of the psychological present according to the estimates of several authors (Pöppel, 1994; Fraisse, 1984; Block, 1979; Michon, 1978). According to Fraisse (1984), within the boundaries of the psychological present "one can speak of the perception of duration, which thereby becomes a quantity whose beginning has not yet been stored in memory" (Fraisse, 1984, p.10). In other words, the duration of the first interval of the second period (B) can be compared directly with the representation of the fourth interval of the first period (A) without involving processes other than working memory (see figure 4). Therefore, only the test of auditory working memory was conducted.

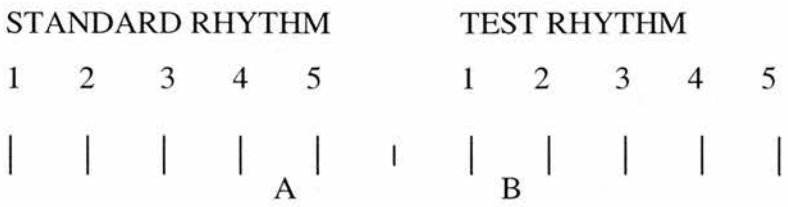

Fig.5: Each vertical line represents a tone of 30 ms. The interval between two tone onsets of the standard rhythm is 700 ms. Between the fifth tone of the standard rhythm and the first tone of the test rhythm there is an interval of 1400 ms. The interval between two tone onsets of the test rhythm may be the same as the standard rhythm or different from the standard rhythm ranging from 500 to 900 ms.

4.2.2. Subjects

Patients from the stroke rehabilitation unit from Drumchapel Hospital, Glasgow, participated in our study. Three neglect patients (three female, mean age 78.3 years) and three non-neglect stroke patients (two female and one male, mean age 77.3 years) were examined[5]. The patients had suffered acute right hemisphere injury as demonstrated by CT-scan without any record of previous cerebral injury (see table 1). Three healthy subjects were examined as control group (two female and one male, mean age 70 years). The difference of age was not significant across the groups (see table 1). There were no auditory deficits in any subject. The patients were also matched for musical background[6].

[5] Formal ethical approval had been obtained by the West Ethics Committee, Glasgow.
[6] Patient no. 1 had studied music privately for several years to become an opera singer but was forced to abandon the plan. Patient no. 4 had trained as a clarinettist and played in the army orchestra for

Table 1: Profile of patients and control subjects in study.

Subject/age/handedness/sex	CT-lesion	Time from cerebral injury at time of testing
Neglect Patients:		
1/79/R/F	R fronto-parietal infarct[7]	2 weeks
2/82/R/F	R deep temporal lobe infarct	1 week
3/74/R/F	R parietal infarct	7 weeks
Non-neglect Patients:		
4/72/R/M	R parietal infarct	5 weeks
5/74/R/F	R subcortical fronto-temporal infarct[7]	2 weeks
6/86/R/F	R subcortical temporal infarct	4 weeks
Control Subjects:		
7/68/R/F-	-	-
8/68/R/F	-	-
9/74/R/M	-	-

Table 2: Patients' and control subjects' performance on star cancellation task and phonological working memory.

	Star cancellation tests 1 2 3 Side and number of stars cancelled			Auditory working memory
Neglect Pts.				
1	R/1	R/17	R/20	18
	L/0	L/0	L/0	
2	R/7	R/11	R/27	19
	L/0	L/0	L/12	
3	R/18	R/20	R/27	19
	L/0	L/1	L/15	
Non-Neglect Pts.				
4	R/27	R/27	R/27	20
	L/27	L/27	L/27	
5	R/27	R/27	R/27	19
	L/27	L/25	L/27	
6	R/27	R/27	R/27	18
	L/27	L/25	L/25	
Control Subjects				
7	Not tested			20
8	Not tested			20
9	Not tested			20

Note. The score in the auditory working memory test refers to the number of correct responses.

several years. He retired from music as a professional but was a keen player in his private time. Subject no. 9 was a trained organist and taught music at school.

[7] The pre-frontal cortex was spared in this patient which allowed us to include the patient in the study.

4.2.3. Apparatus

An apple MacIntosh computer LC 475 controlled all experimental events. It was stationed in a quiet hospital room. All the experiments were conducted in this room and its interior never changed. The program with which the experiment was written was PsyScope 1.1. A closed set of ear phones was used (Sony, MDR CD 550) to present the stimuli.

4.2.4. Design

A mixed design was used. The between subject variable was cerebral damage with three levels (no cerebral damage, damage with unilateral neglect and cerebral damage without neglect). Two dependent variables were measured: The position of the curve which represented the subjects' responses, which is referred to as the bisection point, and the subjects' ability to discriminate the test stimulus, the Weber fraction (see below for further explanation). The independent within variables were the interstimulus interval of the test rhythm with 17 levels (ranging from 500 to 900 ms at 25 ms increments) and the hemisphere to which the test rhythm was presented (2 levels, left and right hemisphere). All subjects were presented with the same stimuli for all conditions.

4.2.5. Stimulus material and procedure

The standard rhythm consisted of five equitone beats with a fixed interval of 700 ms. The test rhythms consisted of five equitone beats with varying interbeat intervals (500 ms, 525 ms, 550 ms, 575 ms, 600 ms, 625 ms, 650 ms, 675 ms, 700 ms, 725 ms, 750 ms, 775 ms, 800 ms, 825 ms, 850 ms, 875 ms, 900 ms). Each single beat was generated by a rectangular sound (2000 Hz) of 30 ms duration.

The experiment started by presenting the standard rhythm to one ear (see app. 8b for instructions to the subjects). The standard interval was marked by the digit "1". The digit was presented on the right side of the screen, right of a central cross. The cross was intended to function as a cue to facilitate perception of the digit. After a delay of 700 ms, the first beep of the series of five beats was delivered. After the fifth beat,

the word "END" appeared on the right side of the screen next to the cross with a 300 ms delay. The standard rhythm was followed by the presentation of a test rhythm. The test rhythm was marked by the digit "2". The digit appeared 400 ms after the word "END" which indicated the end of the standard rhythm. The digit was presented on the right side of the screen, right of a central cross. There was a time interval of 1400 ms between the fifth/last beat of the standard rhythm and the first beat of the test rhythm. In other words, the first beat of the test rhythm formed the seventh beat of the standard rhythm with a missing sixth beat (see figure 5). After the fifth beat of the test rhythm, the word "END" appeared on the right side of the screen next to the cross with a 700 ms delay. The test rhythm was presented to the ear which was different from the ear to which the standard rhythm had been played. The test rhythm was always preceded by the standard rhythm.

After the response "SAME" or "DIFFERENT" was given by the subject, the experimenter pressed the appropriate button of the button box which was hidden behind a screen. The press of the button then delivered the next rhythm pair. The inter-trial interval varied up 10 s. When the subject did not respond, the experimenter would try to prompt the subject by saying "WHAT IS YOUR RESPONSE?" for example. A new rhythm pair was also announced verbally by the experimenter by saying "A NEW RHYTHM PAIR", for example. After the classification of 17 test rhythms, the experiment was repeated as described above with one difference: If the standard rhythm had been played to the left ear and the test rhythms to the right ear, this time the standard rhythm would be presented to the right ear and the test rhythm to the left ear.

At the beginning of each session, the subject was given the following training session. Four rhythm pairs were presented as described above and consisted of the above standard rhythm and a training rhythm. The training rhythms were constructed in the same way as the test rhythms and had an interbeat interval of 300 ms, 500 ms, 900 ms and 1100 ms. The standard rhythm always preceded the training rhythm. In total, the training consisted of four rhythm pairs.

In each experimental session, patients classified between 17 up to 68 test rhythms depending on their clinical condition. The ear to which the test rhythms were presented was alternated during and between session. In total twelve classifications were made for each test rhythm when presented to the left ear and twelve classifications of each test rhythm when presented to the right ear. One session was completed in up to 30 minutes. In total, six up to 24 sessions were held.

4.2.6. Results

A probit analysis was performed that produced a transformed plot of the data. The probit transformed plot allowed the calculation of the 'bisection point' which was defined as the test rhythm which was classified as "same" on 50% of the trials. The difference limen was obtained which was half the difference of the test rhythm classified as "same" on 75% of trials and that classified as "same" on 25% of the trials. The Weber Fraction was calculated by dividing the difference limen by the bisection point (figure 6). The Weber Fraction represents a measure of the subjects' accuracy, i.e. of their ability to discriminate that specific kind of stimuli. Because the reference rhythm was 700 ms and the test rhythms covered the range of 500 ms to 900 ms at increments of 25 ms, two ogive test rhythm curves were obtained for each ear condition (left ear, 500 to 700 ms; right ear, 500 to 700 ms; left ear, 700 to 900 ms; right ear, 700 to 900 ms).

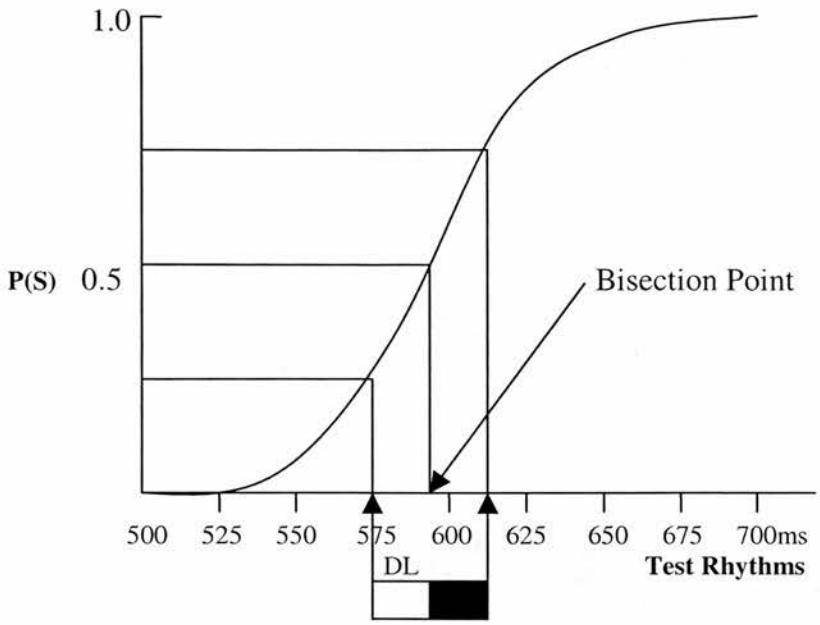

Fig. 6: Example for probit transformed plot of the rhythm task covering test rhythms from 500 to 700 ms. The arrow points to the bisection point. The difference limen (DL in the figure) is half the difference between the test rhythm classified as same 75% and 25% of the times (i.e. half the difference between values on the abscissa corresponding to probability P(S) = 0.75 and to P(S) = 0.25). As a consequence of Weber's Law, to obtain a measure of the subject's ability to discriminate test rhythms, the difference limen has to be weighted based on the individual's bisection point. The Weber Fraction is defined as "difference limen"/"bisection point".

To summarise the motivation for this experiment: We predicted that any rhythm presented to the damaged hemisphere will be perceived as being faster than it is according to objective physical measures. This phenomenon was expected to emerge in both stroke groups with a significantly stronger effect in the neglect group. More specifically, when the reference rhythm is presented to the damaged hemisphere, it will be perceived as quicker than it is because relatively fewer pulses are counted over a unit of time. Consequently, the bisection point of the test rhythms presented to the intact hemisphere where relatively more pulses are counted will shift to the left. Conversely, when the reference rhythm is played to the intact hemisphere, relatively more pulses are counted compared to the damaged hemisphere. The test rhythms are perceived as faster than they are in the damaged hemisphere (relatively fewer pulses are counted). Therefore, relatively slower test rhythms compared to the reference rhythm will be judged as the same and the bisection point moves to the right, i.e. towards the slower rhythms.

The neglect patients and patient no. 6 from the non-neglect group classified test rhythms covering the range from 700 ms to 900 ms so inconsistently that the probit analysis could not produce a meaningful bisection point. Therefore, bisection point data of those patients had to be excluded in the above range.

Position of Bisection Point

- Bisection point for fast rhythms after presentation of the reference rhythm to the left and right ears:

When the reference rhythm was presented to the left ear, the mean bisection point of the fast rhythms (500 to 700 ms) was at 634 ms for the control group, 628.6 ms for the non-neglect group and 627.6 ms for the neglect group (table 3). A non-parametric Jonkheere test for ordered alternatives was performed (N < NN < C). No significant result emerged across the groups (J = 16, $p > 0.05$). A non-parametric Kruskal-Wallis test confirmed the result ($\chi^2 = .625$, $d.f. = 2$; $p > 0.05$).

After presentation of the reference rhythm to the right ear, the mean bisection point was at 633 ms for the control group, 633 ms for the non-neglect group and 646.3 ms for the neglect group (table 3). No significant bisection point shift was revealed in a Jonkheere test for ordered alternatives (C < NN < N; $J = 19$, $p > 0.05$). The data were not significant in the Kruskal-Wallis test either ($\chi^2 = 3.2$, $d.f. = 2$, $p > 0.05$).

Table 3: Mean bisection point for test rhythms from 500 ms to 700 ms with a reference rhythm of 700 ms.

	Reference Rhythm to Left Ear	Reference Rhythm to Right Ear
Neglect Group	627.6 ms	646.3 ms
Non-Neglect Group	628.6 ms	633 ms
Control Group	634 ms	633 ms

Comparing the bisection point between the two ear conditions, the position of the bisection was virtually the same for the control group; irrespective of side of presentation (non-paramentric Friedman test: $\chi^2 = 0.33$, $d.f. = 1$, $p > 0.05$). Nevertheless, as predicted, both the non-neglect and the neglect group had a bisection point which was greater in the right ear condition. Furthermore, the

difference between the two ear conditions was more pronounced for the neglect group (19.3 ms versus 5 ms). The shift to the right was not significant in the non-neglect group (non-paramentric Friedman test: $\chi^2 = 0.001$, $d.f. = 1$, $p > 0.05$). However, in the neglect group, the result was marginally significant (Friedman test: $\chi^2 = 3$, $d.f. = 1$, $p = 0.08$).

In summary, both in the non-neglect group and the neglect group, a rightward shift of the bisection point was detected between the different ear conditions whereas the bisection point position of the control group remained the same irrespective of side of stimulus presentation.

- Bisection point for slow rhythms after presentation of the reference rhythm to the left and right ears:

In the range of test rhythms from 700 ms to 900 ms, the responses of the neglect group and also of one patient (no. 6) in the non-neglect group were so erratic that the obtained bisection point had no meaning. The data of these patients were therefore excluded from the analysis of bisection point position for the slower test rhythm range. Between the two remaining groups no significant shifts of bisection point were observed, either after presentation of the reference rhythm to the left ear (Kruskal-Wallis, $\chi^2 = 1.33$, $d.f. = 1$, $p > 0.05$) or after presentation of the reference rhythm to the right ear (Kruskal-Wallis, $\chi^2 = 0.78$, $d.f. = 1$, $p > 0.05$). The mean bisection point of the control group was at 747 ms after presentation of the reference rhythm to the left ear. For the same presentation condition, the bisection point was calculated at 755 ms for the two non-neglect patients. When the reference rhythm was presented to the right ear, the bisection point was at 749. 6 ms for the control group and at 757 for the two non-neglect patients (table 4).

Table 4: Mean bisection point for test rhythms from 700 ms to 900 ms with a reference rhythm of 700 ms.

	Reference Rhythm to Left Ear	Reference Rhythm to Right Ear
Control Group	747 ms	749.6 ms
Non-Neglect Group	755 ms	757 ms

The difference in the position of the bisection point was virtually the same between the left and right ear presentation conditions for the non-neglect and the control group (2 ms and 2.6 ms, respectively). The graphs below represent the performance of each group for each presentation condition (fig. 7, 8, 9 a, b, c, d).

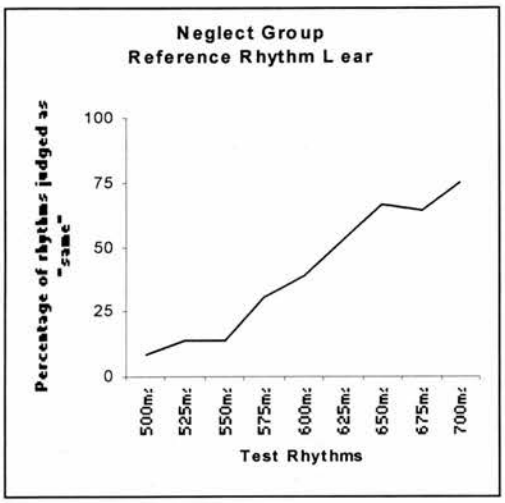

Fig. 7a: Neglect group. Fast rhythms. Left ear condition.

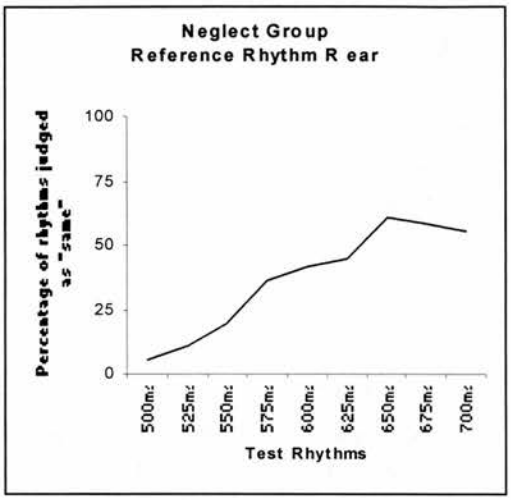

Fig. 7b: Neglect group. Fast rhythms. Right ear condition.

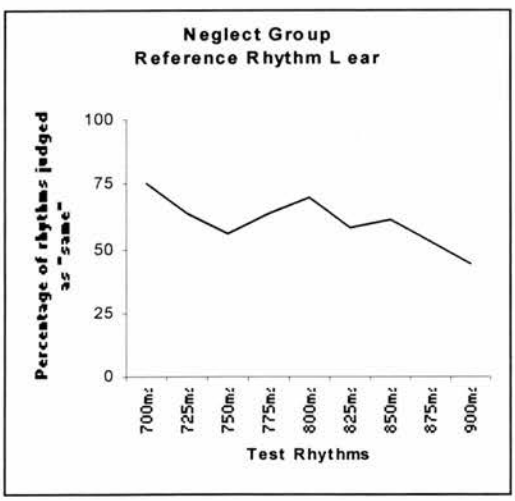

Fig. 7c: Neglect group. Slow rhythms. Left ear condition.

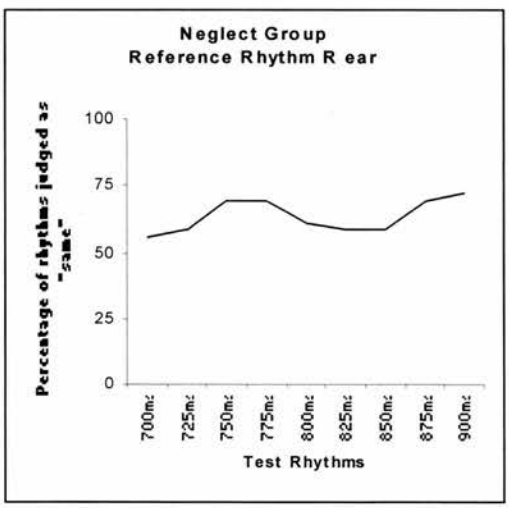

Fig. 7d: Neglect group. Slow rhythms. Right ear condition.

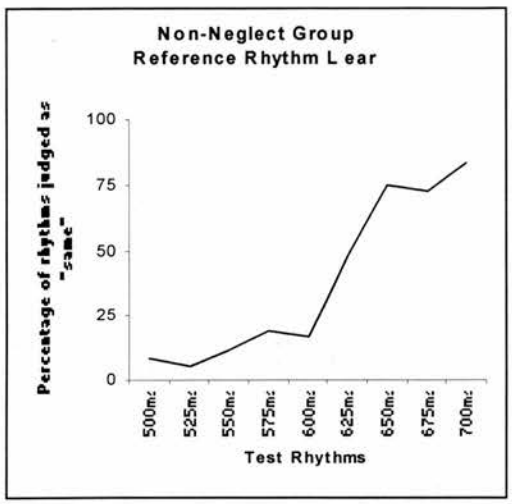

Fig. 8a: Non-neglect group. Fast rhythms.

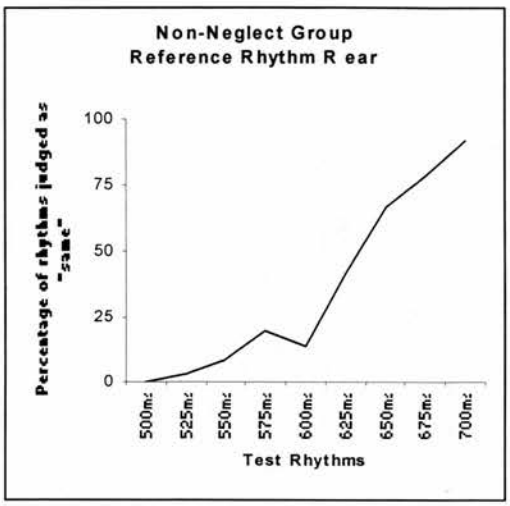

Fig. 8b: Non-neglect group. Fast rhythms.

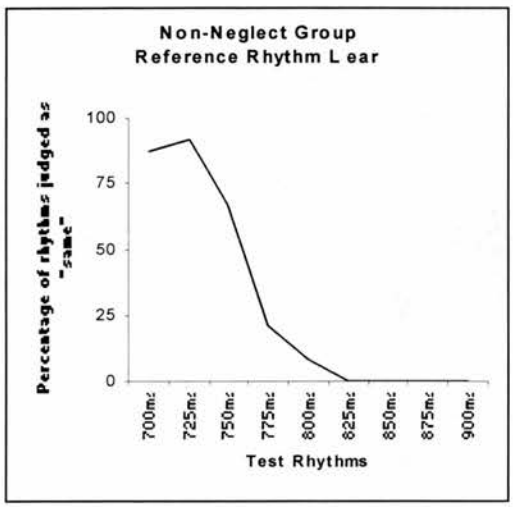

Fig. 8c: Non-neglect group. Slow rhythms.

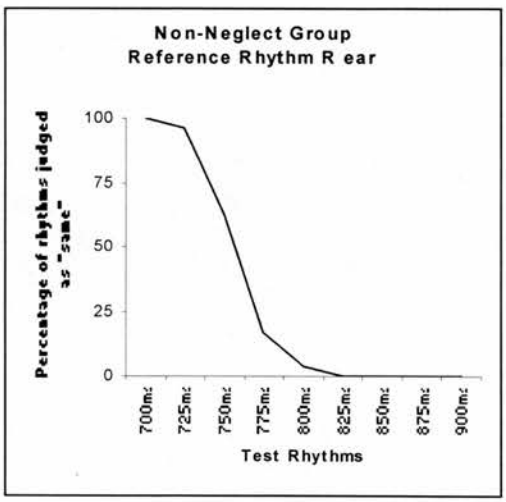

Fig. 8d: Non-neglect group. Slow rhythms.

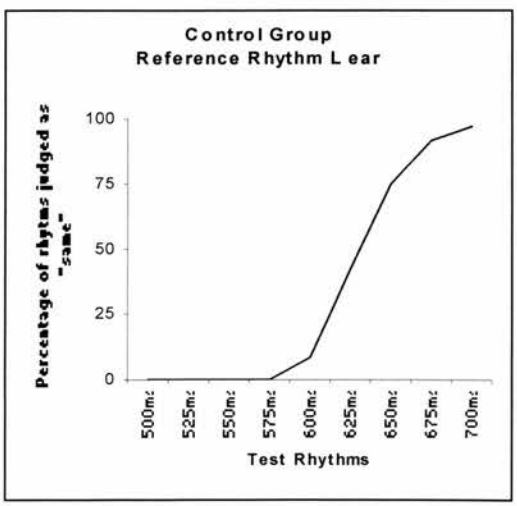

Fig. 9a: Control group. Fast rhythms.

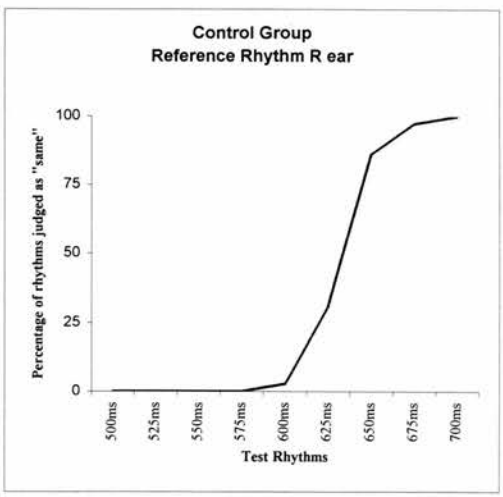

Fig. 9b: Control group. Fast rhythms.

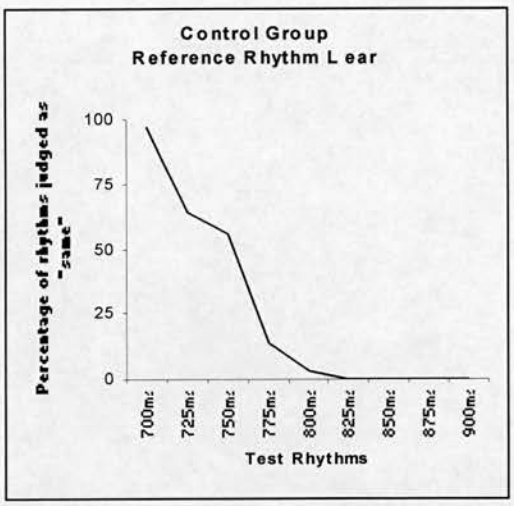

Fig. 9c: Control group. Slow rhythms.

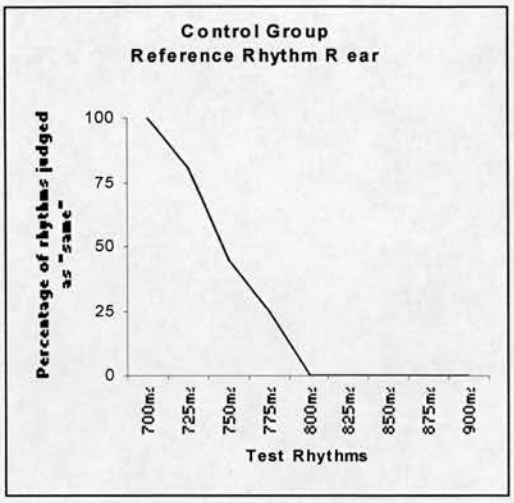

Fig. 9d: Control group. Slow rhythms.

Weber Fraction

The Weber Fraction represents a measure of the subject's ability to discriminate this specific kind of stimulus. A series of non-parametric Jonkheere tests for ordered alternatives was performed to compare the performance of the three groups for fast and slow rhythms and for the left and right ear conditions.

- Slow and fast rhythms after presentation of the reference rhythm to the left ear:

For test rhythms of the range from 500 ms to 700 ms after presentation of the reference rhythm to the left ear the mean Weber Fraction was 0.029 for the controls, 0.068 for the non-neglect patients and 0.1 for the neglect group ($C < NN < N$, $J = 23$, $p < 0.05$). For the left ear condition and rhythms from 700 ms to 900 ms, the mean Weber Fraction was 0.026 for the control group, 0.1 for the non-neglect group and 0.38 for the neglect patients ($J = 23, p < 0.05$) (table 5).

Table 5: Mean Weber Fraction for presentation of reference rhythm to left ear.

	Test Rhythms 500 - 700ms	Test Rhythms 700 - 900ms
Neglect Group	0.1	0.38
Non-Neglect Group	0.068	0.1
Control Group	0.029	0.026

For the fast test rhythms, a Kruskal-Wallis test revealed no significant difference between the Weber Fraction of the control group and the non-neglect group (χ^2 = 1.26, *d.f.* = 1, $p > 0.05$) between the non-neglect group and the neglect group (χ^2 = 0.44, *d.f.* = 1, $p > 0.05$) but a significant difference between the control and the neglect group (χ^2 = 3.97, *d.f.* = 1, $p < 0.05$). The neglect group's ability to discriminate test rhythms ranging from 500 to 700 ms was therefore significantly worse than the control group's ability.

As for the slow rhythms, there was no significant difference between the control group and the non-neglect group (χ^2 = 1.67, *d.f.* = 1, $p > 0.05$) between the non-neglect group and the neglect group (χ^2 = 1.22, *d.f.* = 1, $p > 0.05$) but a significant difference between the control and the neglect group (χ^2 = 3.97, *d.f.* = 1, $p < 0.05$).

In summary, for both the fast and the slow rhythms the neglect group discriminated the stimuli significantly worse than the control group.

- Slow and fast rhythms after presentation of the reference rhythm to the right ear:

For test rhythms of the range from 500 ms to 700 ms after presentation of the reference rhythm to the right ear the mean Weber Fraction was 0.018 for the controls, 0.05 for the non-neglect patients and 0.13 for the neglect group (C < NN < N; $J = 26$, $p < 0.005$). For the right ear condition and rhythms from 700 ms to 900 ms, the mean Weber Fraction was 0.02 for the control group, 0.08 for the non-neglect group and 0.4 for the neglect patients ($J = 24$, $p = 0.01$) (table 6).

Table 6: Mean Weber Fraction for presentation of reference rhythm to right ear.

	Test Rhythms 500 - 700ms	Test Rhythms 700 - 900ms
Neglect Group	0.13	0.4
Non-Neglect Group	0.05	0.08
Control Group	0.018	0.02

For the fast rhythms, a Kruskal-Wallis test revealed no significant difference between the Weber Fraction of the control group and the non-neglect group ($\chi^2 = 2.4$, *d.f.* = 1, $p > 0.05$) between the non-neglect group and the neglect group ($\chi^2 = 2.4$, *d.f.*

= 1, $p > 0.05$) but a significant difference between the control and the neglect group ($\chi^2 = 4.5$, *d.f.* = 1, $p < 0.05$). The neglect group's ability to discriminate test rhythms ranging from 500 to 700 ms was therefore significantly worse than the control group's ability. As for the slow rhythms, there was no significant difference between the control group and the non-neglect group ($\chi^2 = 0.22$, *d.f.* = 1, $p > 0.05$), between the non-neglect group and the neglect group ($\chi^2 = 1.22$, *d.f.* = 1, $p > 0.05$) but a significant difference between the control and the neglect group ($\chi^2 = 1.22$, *d.f.* = 1, $p < 0.05$).

In summary, for both the fast and the slow rhythms the neglect group discriminated the stimuli significantly worse than the control group irrespective of side of presentation. Furthermore, the non-neglect group's performance was not significantly better than the one of the neglect group which suggests some deficit in the discrimination of the stimuli. However, this result has to be attributed to the high Weber Fraction of non-neglect patient no. 6 whose performance was almost as bad as the performance of the neglect patients. The remaining two non-neglect patients on the other hand performed almost as well as the normal control group. Therefore, it would be misleading to claim a deficit to discriminate the stimuli for the whole non-neglect population.

- The discrimination of fast versus slow rhythms:

Interestingly, the neglect group's Weber Fraction was greater for test rhythms covering the range from 700 ms to 900 ms, i.e. their ability to discriminate the slower test rhythms was worse than the discrimination of the faster rhythms (tables 5, 6). The effect emerged both in the left and right ear condition and approached significant levels (Friedman test, $\chi^2 = 3$, *d.f.* = 1, $p = 0.08$ for both ear conditions). The lack of accuracy in the judgement of the slow test rhythms is reflected by an almost horizontal graph instead of a steep s-shaped curve (fig. 7 c, d). Although the Weber Fraction for slower rhythms increased in the non-neglect group too, the difference was not significant (reference rhythm to left ear, Friedman test, $\chi^2 = 0.001$, *d.f.* = 1, $p > 0.05$; reference rhythm to right ear, $\chi^2 = 0.001$, *d.f.* = 1, $p > 0.05$). Similarly, the control group was equally accurate to discriminate slow rhythms as fast rhythms

(reference rhythm to left ear, Friedman test, $\chi^2 = 2$, $d.f. = 1$, $p > 0.05$; reference rhythm to right ear, $\chi^2 = 1$, $d.f. = 1$, $p > 0.05$).

- The discrimination of fast and slow rhythms: left versus right hemisphere

No significant differences of the Weber Fractions were detected between the left and right ear condition in the neglect group for fast and slow test rhythms (neglect group, 500 to 700 ms, Friedman test, $\chi^2 = 0.33$, $d.f. = 1$, $p > 0.05$; 700 to 900 ms, Friedman test, $\chi^2 = 0.33$, $d.f. = 1$, $p > 0.05$). In the non-neglect group, there was no significant difference between the left and right ear condition for the fast rhythms (500 to 700 ms, $\chi^2 = 2$, $d.f. = 1$, $p > 0.05$). For the slow rhythms, the performance was more accurate when the reference rhythm was presented to the right ear/left hemisphere. However, the difference only approached significance (700 - 900 ms, $\chi^2 = 3$, $d.f. = 1$, $p = 0.08$). A similar result emerged for the control group but in this case the right ear/left hemisphere advantage of the reference rhythm approached significance for the fast rhythms (500 to 700 ms, $\chi^2 = 3$, $d.f. = 1$, $p = 0.08$). There was no difference in accuracy for the slow rhythms 700 to 900 ms, $\chi^2 = 2$, $d.f. = 1$, $p > 0.05$).

In summary, the neglect group performed equally badly independent of the ear to which the reference and test rhythms were presented. For the non-neglect and control group a trend emerged that suggested improved accuracy when the reference rhythm was presented to the left hemisphere and the test rhythms to the right hemisphere. The effect only approached significant levels; in the case of the non-neglect group for slow test rhythms and in the control group for fast test rhythms.

4.2.7. Discussion

We have investigated the perception of fast (interstimulus interval 500 to 700 ms) and slow test rhythms (interstimulus interval 700 to 900 ms) in stroke patients with and without neglect and in a normal control group.

There are two main findings: The first one fits the hypotheses based on our temporal diplopia theory. The results have demonstrated that for fast rhythms there was a shift of the bisection point to the right both in non-neglect and neglect patients when the reference rhythm was presented to the left hemisphere and the test rhythms to the

right hemisphere compared to the condition of reference rhythm presentation to the right hemisphere and test rhythm presentation to the left hemisphere. We have claimed that the right hemisphere is slowed down after cerebral injury. According to scalar timing theory, fewer pulses are accumulated in a slowed down hemisphere. Consequently, when the reference rhythm of an interstimulus interval of 700 ms is presented to the left hemisphere, more pulses are accumulated compared to a test rhythm with the same interstimulus interval played to the damaged right hemisphere. Thus, the bisection point will be more likely to intersect with slower rhythms, i.e. with rhythms of longer interstimulus intervals to accumulate the 'required' number of pulses for the patient to make a "same" judgement. The bisection point therefore shifts to the right. This hypothesised right-shift was demonstrated in both stroke groups. The shift was not significant in the non-neglect group but it approached significance in the neglect group. The fact that the effect was less pronounced in the non-neglect group is consistent with the predictions of our theory as we have claimed that slowing down is more severe in the neglect group (based on the neurophysiological evidence presented in the fourth chapter).

The second main result of our study is that both stroke groups displayed deficits in the discrimination of the test rhythms. The impairment was much more severe in the neglect group whose Weber Fraction was significantly greater than the ones of the control group for fast and slow rhythms irrespective or the side of presentation. This result also replicates the finding of an increased Weber Fraction that was reported in the time bisection performance of the neglect group (chapter five; see also Marshall & Halligan, 1989). The mean Weber Fraction of the non-neglect group was not significantly better than that of the neglect group which suggests some impairment in the discrimination of the test rhythms. However, one non-neglect patient (no. 6) produced atypically high Weber Fractions compared to the remaining two non-neglect patients so that a claim of an impairment in the whole non-neglect group would be misleading. What is more, the performance in all three groups was not significantly different between the left and right ear presentation. That is, there were no differences whether the standard rhythm was presented to the left ear and then the test rhythm to the right ear or vice versa. These results are consistent with the

absence of clear laterality effects in the rhythm perception literature. Previous studies have suggested a left-hemisphere specialisation for auditory temporal and rhythmic processing (Effron, 1963; Robinson & Solomon, 1974; Mavlov, 1980; Robin et al., 1990; Platel et al., 1997). Others did not find evidence for specialisation (Peretz, 1990; Liégois et al., 1998) whereas Penhune et al. (1998) stressed the specific role of the right anterior secondary auditory cortex in the retention of auditory tonal patterns. In sum, there is controversy in the literature about a clear lateralisation to either the left or the right hemisphere. Also, the above studies refer to subjects with low musical aptitude. It appears that musically trained individuals display fewer laterality effects in rhythm perception than non-musical subjects (Gaede et al., 1978; Bradshaw & Nettleton, 1981).

One might argue that potential working memory effects would influence the way stroke patients respond depending on whether the standard rhythm is first presented to the intact or the damaged hemisphere. Accordingly, one could hypothesise a deterioration when the standard rhythm is played to the damaged hemisphere because the memory trace tends to be more unstable than the one generated in the intact hemisphere. When the first beat of the test rhythm is presented after 1400 ms (figure 5) following the standard rhythm, the representation of the standard rhythm is not as accurate anymore and the classification of the test rhythms will consequently be not as precise. Conversely, when the standard rhythm is represented in the intact hemisphere with intact working memory, the test rhythms projected into the damaged hemisphere will be classified more easily because a decision can be made almost immediately after two or three intervals. A hemispheric difference is conceivable for this reason. Such a difference, albeit only marginally significant, was observed in our non-neglect subjects for the slow rhythms. However, the neglect group did not produce any differences between the two ear conditions at all. Absence of a difference in the latter case could be explained by the fact that the overall working memory deficit was too severe.

An additional finding was also that the ability of the neglect group to discriminate slow rhythms was reduced compared to fast test rhythms, although the difference only approached significant levels. This effect was independent of the side of presentation. A similar trend was observed in non-neglect patient no. 6 who

produced a Weber Fraction comparable to the ones of the neglect group. The reason for the atypically high Weber Fractions in patient no. 6 might lie in past neurological damage which has escaped documentation. Nothing in the past medical history was suggestive of previous defects. The deficit of the neglect group and non-neglect patient no. 6 was such that no bisection point data could be obtained for the slow rhythms. The analysis of the bisection point position in the remaining two non-neglect patients and the three control patients did not replicate the right shift observed in the non-neglect group when the reference rhythm was presented to the right ear. Therefore, the bisection point data for the slow rhythms were inconclusive with regard to our hypothesis.

What are the underlying reasons for the impaired ability to discriminate slower rhythms in the neglect group and non-neglect patient no. 6? Griffiths et al. (1997) presented a single case study of a patient who had suffered a right hemisphere infarct affecting the temporal and parietal cortices. The patient complained of a lack of musical appreciation. Visuo-spatial tests suggested that the patient also suffered from unilateral neglect. The patient was tested in a binaural tone sequence task where two pairs of three tones were presented. For one pair, the two tone sequences were identical, while in the other pair the second tone differed in frequency between the two sequences. The rate at which the tones were presented was varied. In the slow tone sequence discrimination task, three notes each of duration of 200 ms were presented over an interval of 650 ms. In the rapid tone sequence task, three notes of the duration of 85 ms were presented over 260 ms. The results showed that the patient was able to discriminate a change in the frequency of the second note when the rate at which the tones were presented were slow which demonstrated that he could discriminate different tone frequencies. Interestingly, the patient performed at chance levels for the rapid sequences.

Griffiths et al. (1997) concluded that the deficit might be caused by a perceptual impairment. The claim is supported by evidence that the temporal cortex plays a crucial role in the retention of rhythmic patterns (Liégois-Chauvel et al., 1998; Nishitani et al., 1998; Penhune, 1999). However, postulating a perceptual impairment does not account for the fact that the patient was able to discriminate slower rhythms.

Furthermore, disrupted functioning of auditory working memory does not explain the observed behaviour as the performance of the neglect patient deteriorated with *decreasing* tone sequence intervals. In this patient, there was no evidence of an impaired auditory working memory which was consistent with the neuroanatomical record of the patient's lesion. The pre-frontal cortex and therefore working memory function which has increasingly been associated with the pre-frontal lobe (Zatorre et al., 1994; D'Esposito et al., 1995, 1998; Knight et al., 1999) appeared to have been spared in this case unless one were to argue that a temporal-pre-frontal neocortical network is critical for the transient storage of auditory stimuli (Alain et al., 1998). It would be interesting to see how Griffiths et al.'s patient (1997) would have performed for tone sequences over 650 ms. The interval of 650 ms, i.e. the duration of the entire slow tone sequence, is only just about as long as one of fast interstimulus rhythm intervals used in our study. We hypothesise that the patient's performance would deteriorate for longer stimulus sequences as it has been observed in the above experiment. Our neglect patients performed better with test rhythms where one stimulus interval was between 500 and 700 ms long. Altogether, four stimulus intervals were presented. In contrast, stimulus intervals ranging from 700 to 900 ms caused problems to the neglect patients and to one of the non-neglect patients.

The data suggest that in our study both neglect and one non-neglect stroke patient displayed some impairment of the auditory working memory which became more obvious with an increase of test rhythm duration - despite an intact pre-frontal lobe. Our model is consistent with the proposals of Sarnthein et al. (1998) who have claimed that working memory involves the synchronisation between the prefrontal and posterior association cortices by phase-locked, low-frequency (4 to 7 Hz) brain activity. We have postulated that in stroke patients both intra- and interhemispheric synchronisation is impaired. Therefore some degree of working memory deficit is accounted for in patients following cerebral damage despite intact pre-frontal cortices. As for Griffiths et al.'s patient (1997), tentatively it could be suggested that his impairment for fast tone sequences is caused by the fact that the stimuli are 'over' before the subject can process them adequately or, in the framework of our theory, neuronal processing is too much slowed down. In addition, attentional deficits can

never be excluded as a confounding factor, particularly in stroke patients with neglect.

Consequently, the above interpretation of the observed rightward shift could be criticised for not taking attentional interference into account. The interference effect describes the fact that when normal subjects allocate attention to non-temporal information, the perceived perception of the duration shortens (Brown, 1997). If one claimed that less attentional capacity is available in the damaged hemisphere of both the neglect and non-neglect group, we would expect the observed rightward shift after presentation of the reference rhythm to the right ear. Similarly, if the working memory trace of the test rhythm were subject to decay, a rightward shift would occur. However, interference from working memory deficits was minimised by subjecting all stroke patients to an auditory working memory test. Furthermore, at least for the non-neglect group, attentional and working memory interference effects can be excluded as the underlying mechanism for the right shift. The Weber fractions of the non-neglect patients were not significantly different from the Weber Fractions of the control group. That is, their ability to discriminate the target stimulus was not significantly worse than the discrimination of the control subjects. We therefore interpret the rightward shift as compatible with the claim that neuronal processing is slowed down in the damaged hemisphere.

4.2.8. Conclusion

Our study has presented novel methodology to assess rhythm perception in stroke patients with and without neglect. The results have provided data consistent with the claim that the damaged hemisphere is slowed down after cerebral damage. Our data have also shown that the observed changes in rhythm perception are more pronounced in neglect patients. These findings fit the hypotheses made by our temporal diplopia theory of unilateral neglect which claims that interhemispheric desynchronisation is due to unilateral slowing down of neuronal processing. A second finding was that the neglect patients were impaired in their ability to discriminate the test rhythms. The effect was particularly severe for the slower test rhythm category. The data suggest that impaired auditory working memory and

attentional processes were the underlying mechanisms for the poor performance with slow rhythms. These findings have practical implications for future rhythm perception studies involving neglect patients. These subjects seem to possess only a very narrow time window in which temporal structures can be discriminated before working memory and attentional deficits make processing impossible.

Chapter Seven

The Inspection Time Paradigm

In this chapter, the inspection time paradigm will be presented. We will first examine the theoretical background of the experiment and then discuss the obtained results. The purpose of the experiment was to investigate asymmetries in temporal resolution across hemispheres in stroke patients with and without neglect.

1. The inspection time paradigm

We will start with the description of the classical inspection time experiment. The stimulus of this two-choice discrimination task is shown in figure 1a, the so-called pi figure.

a)  b) 

Fig. 1: a) The standard inspection time stimulus, the pi figure.
b) The backward mask used for the pi figure.

There are two versions of this stimulus. One has the long line on the right side, and one has the long line on the left. The discrimination task requires a judgement as to the side on which the long line was presented. Provided that visual acuity is normal, subjects have no difficulties in this task since the size of the two vertical lines subtends an angle that poses no problem for the visual system (Deary & Stough, 1996). A backward mask (figure 1b) follows the pi figure to stop any processing of information from iconic storage. The time interval that elapses between the beginning of the display of the pi figure and the presentation of the backward mask is

called the stimulus onset asynchrony (SOA). The inspection time of a subject can therefore be defined as the minimum stimulus onset asynchrony necessary to discriminate the stimulus at a given level of accuracy (Sadler & Deary, 1996). Depending on the length of the SOA ranging from several hundred milliseconds to below 10 ms, the discrimination task can be very easy or extremely difficult dropping the performance to chance levels. The subject is told that speed of reaction is not relevant. A decision should be made at the subject's own time.

The concept of the inspection time paradigm, a theory of discriminative judgements, was proposed by Vickers and his colleagues (Vickers 1970, 1979; Vickers et al., 1972; Vickers & Smith, 1986) and is based on the accumulator model. This model is firmly rooted in the tradition of the *psychological moment*. A second aspect of the inspection time rationale deals with the interaction of information processing and masking.

1.1. The Psychological Moment Theory

This school of thought assumes that psychological processing is discontinuous, i.e. that information is packed into a series of temporally constrained samples. A considerable number of researchers have subscribed to this approach of information processing (e.g. Stroud, 1955; White, 1963; Shallice, 1964; Kristofferson, 1967; Michon, 1967; Pöppel, 1994, 1995).

Stroud (1955) has been credited with the introduction of the term *psychological moment* although other writers like Bergson (1913) used the term *moment* as well but less consistently (White, 1963). Stroud's concept of a moment included all types of information and implied a central location of processing. "A Stroudian moment encompasses at least all of man's awareness, probably a major fraction of his nervous activity, and possibly most of the activity of the entire organism at a given instant" (Stroud, 1955, p.207). Later Shallice (1964) who focused on the processing of sensory information introduced the term *perceptual moment* as a more parsimonious version (or henceforth PM).

The theory of discontinuous information processing which was formulated most explicitly by Stroud (1955) claimed further that temporal order information of events

does not exist when these events fall within the boundaries of a moment, for example as a result of a summation process. That is, all events falling within a moment are perceived as occurring at the same time. Successive perception of events is achieved only when the events coincide with at least two different moments. The moment or "sample length thus becomes an irreducible unit, or quantum, of subjective duration – the perceptual moment" (Allport, 1968, p.395).

White (1993) attributed four dimensions to the *moment*: Psychological versus perceptual, autonomous versus triggered, instantaneous versus integrating and discrete versus travelling. The distinction between psychological and perceptual has been mentioned above. As for the second dimension, Stroud (1955) postulated that PM be autonomous, that is that the timing of the PM is centrally organised and independent of the information input. The majority of the researchers subscribe to the property of autonomy (White, 1993) apart from Pöppel (1994; 1995) who supports the view of a "stimulus-triggered or instantaneously entrained system state" (Pöppel, 1994, p.192). The difference between instantaneous and integrating can be described as follows. In an instantaneous system, information is only sampled when it coincides temporally and spatially with the beginning of the PM whereas in the integrating system information is encoded independent of the beginning of the PM and "sampled information [is] subjected to an averaging or integrating process" (White, 1993, p.190). The last dimension of the PM discussed by White (1993) applies to the dichotomy of discrete versus travelling. Normally, the PM is regarded as discrete or non-overlapping. Allport (1968) proposed the theory of the *travelling* moment which implies the continous running moment of sensory input with overlapping representations, i.e. a single event will be recorded in two or more moments and two successive events might fall within one moment and might still be perceived as successive as long as they are represented in two different moments at an earlier or later stage (White, 1993). In the discrete moment hypothesis (e.g. Stroud, 1955), an event will only be represented in one moment once and two single events will be judged simultaneously when they are recorded within one moment. Allport (1968) gives the following analogy to illustrate his approach: "To a man standing on the platform, the occupants of a passing train are revealed compartment by compartment as each window draws by. His glimpses of the interior of the train

are essentially discontinuous in time. To an observer in one of the compartments, on the other hand, the field of view is always bounded by his own carriage window. Now, elements of the passing scene enter his view continuously from one side of the window, while others drop out of it at the other. Given a temporal rather than a spatial extension, the moving window analogy corresponds to the idea of a continuous 'travelling moment' (Allport, 1968, p.396).

The concept of the PM is an integral part of the inspection time rationale and the accumulator model which will be discussed in the next section.

1.2. The accumulator model and the inspection time

The idea of inspection time (IT) grew out of the framework of an accumulator model of comparative judgement (Vickers 1970, 1979; Vickers et al., 1972; Vickers & Smith, 1986). Figure 2 (from White, 1993) illustrates the components of the specific version of the model which was modified by Vickers and Smith (1986).

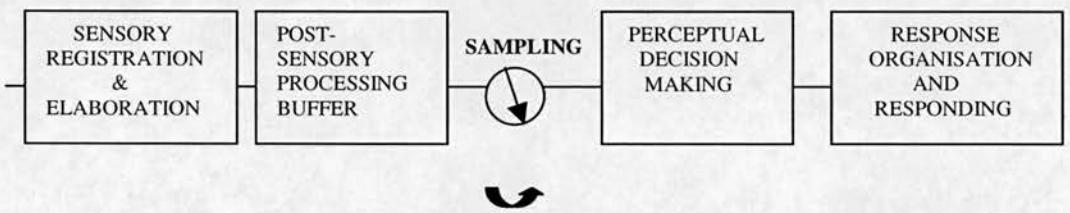

Fig.2: Intermittent sampling model

The accumulator model assumes that discrete samples or observations are taken at a steady rate from a post-sensory processing buffer, with each observation taking an equal amount of time. The representation in the buffer is superimposed on a background of neural noise from both internal and external sources. The information gained through each sampling process is transferred to a subsequent decision making stage where information is accumulated until a decision is reached. The decision is followed by a response. The described sampling processes is illustrated by a rotating arrow in figure 2. Sampling is instantaneous and starts when the arrow is in horizontal position pointing to the right. The sampling process is finished when the arrow has rotated through 360 degrees.

Vickers and Smith (1986) defined IT as "the time required by a subject to make a single observation or inspection of the sensory input" (Vickers & Smith, 1986, p.609). The IT is supposed to be constant with wide ranging individual differences and its value is estimated to be around 100 ms (Vickers et al., 1972). It is impossible to measure the number of observations which a subject takes when he/she is processing a complex stimulus. Consequently, if one does not know the number of observations taken by a subject, IT cannot be calculated. For this reason, a paradigm of perceptual discrimination was developed which was meant to be sufficiently simple that a single observation is enough to achieve a reliable level of accuracy of discrimination. This paradigm is the above described inspection time experiment with a pi figure as stimulus (fig.1).

The time T_A it takes to arrive at a decision and make the response R_A when more complicated stimuli than the pi figure is involved is expressed by the following formula (Vickers & Smith, 1986, p.614):

(1) $T_A = \lambda N_A + t_o$

Where t_o is "a measure of residual, or non-decision time, associated with movement time and delays along sensory pathways" (Vickers & Smith, 1986, p.614), N_A is the number of observations needed to make a correct decision and λ stands for IT, i.e. the time needed for a single observation.

This section was preceded by a short introduction to the theories of the psychological/perceptual moment because Vickers et al. (1972) postulated that "the perceptual moment can be regarded as corresponding to inspection time" (Vickers et al., 1972, p.275).

Following White's (1993) analysis, the perceptual moment within Vicker and colleagues' framework should have the following additional properties: It should be instantaneous rather than integrating, autonomous rather than triggered and discrete rather than travelling.

1.3. Inspection time and backward masking

In the classical inspection time paradigm described above a pattern mask follows the pi stimulus. More precisely, the onset of the mask is simultaneous with the offset of the pi stimulus. The motivation for using a backward mask is addressed by Nettelbeck (1985, p.113): "Without the introduction of the mask, visual persistence would permit additional processing that could not be prevented or controlled. However ... it is assumed that when exposure of this pattern mask closely follows the presentation of the target figure, sensory information relevant to the discrimination is limited to subsequent processing for the duration between target onset and mask onset...".

This definition implies, first, that the stimulus representation in the post-sensory processing buffer is available in a complete and unchanged form and, second, present for the sampling process for a period exactly equal to the SOA (White, 1993). These two claims rest on the so-called interruption theory of masking. Interruption theory is an all-or-none approach in that it postulates that the backward mask wipes out completely the representation of the target stimulus and its only effect is the limitation of sampling time of the target stimulus.

The alternative view is represented by the integration theory. This theory claims that "stimulus degradation is a matter of degree" depending on mask features like energy and structure. "The second major difference between interruption and integration is that interruption theory, as the name implies, assumes that only the second of two stimuli can have a masking effect, while integration theory makes no such assumption" (White, 1993, p.196). Advocates of the integration theory therefore question the validity of backward masking techniques (White, 1993).

To summarise, first, it is claimed by Vickers and colleagues that the IT is a measure of speed of post-sensory processing (Vickers et al., 1972; Vickers and Smith, 1986) and that this processing occurs centrally (Nettelbeck et al., 1984). The latter was demonstrated in an inspection time task that was performed under two conditions. In the binocular condition, the target and the backward mask were presented to both eyes. In the dichoptic condition, target and mask were presented each to different

eyes. The claim was that in the latter case, only central masking can occur. It was argued that if the same process applies to the discrimination task with normal binocular presentation, the results under both dichoptic and binocular procedures should be the same. This prediction was confirmed by the data (Nettelbeck et al., 1984).

Second, the time of availability for processing of the target stimulus is accurately controlled by the application of a backward mask. Depending on the structure of the target stimulus, the stimulus is processed after one sampling period (the inspection time) or a whole-number multiple of the inspection time.

A number of studies provided evidence against the perceptual moment theory (e.g. Di Lollo & Wilson, 1978; Ulrich, 1987) and according to White (1993, p.191) it "failed to win general acceptance". On the other hand, in recent years Pöppel and his colleagues (e.g. Pöppel et al., 1990; Pöppel, 1994; 1995) have produced evidence in favour of the perceptual moment theory.

In a theoretical paper, White (1993) dismissed the inspection time rationale as a paradigm that only taps sensory processing mechanisms as opposed to post-sensory processes. Deary et al. (1993) demonstrated a practice effect over long periods of testing of inspection time, an observation which was not predicted by Vicker's theory. However, the inspection time paradigm has witnessed a recent revival particularly for its correlation with performance in IQ-tests (e.g. Nettelbeck & Lally, 1976; Brand, 1981, 1984; Brand & Deary, 1982; Deary & Stroud, 1996)

2. The modified inspection time paradigm

2.1. Introduction

In the inspection time experiment of the current study, the classical pi figure was not used. Instead a set of stimuli was chosen that Hellige et al. (1989) had developed in their study which investigated hemispheric interaction in normal subjects. The stimuli were a set of consonant-vowel-consonant non-word syllables (e.g. "GES"). The reason for this decision was that the pi figure might enforce a well known behavioural particularity in neglect patients to persevere with their responses. Presentation of a more complex stimuli might alleviate that behaviour. Also, a three

letter non-word consists of three components as opposed to the two legs of the pi figure. The chances of the patient perceiving at least parts of the stimulus were therefore increased.

The motivation for this experiment was, first, to investigate the required time T_A for each hemisphere to perceive a given stimulus correctly. The hypothesis was that neglect patients require a much longer T_A for stimuli presented on the side of their neglected visual field compared to non-neglect patients. However, it is also predicted that stroke patients without neglect will produce a significantly longer T_A compared to normal control subjects but a shorter T_A compared to neglect patients.

Our hypothesis is rooted in the theory of the accumulator model (fig.2). T_A is the time it takes to arrive at a decision and make the response R_A when more complicated stimuli than the pi figure are involved. This relationship is expressed by the following formula (see above; Vickers & Smith, 1986, p.614):

(1) $T_A = \lambda N_A + t_o$

Where t_o is "a measure of residual, or non-decision time, associated with movement time and delays along sensory pathways" (Vickers & Smith, 1986, p.614), N_A is the number of observations needed to make a correct decision and λ stands for IT, i.e. the time needed for a single observation. In chapter four, we have presented evidence for the claim that in the damaged hemisphere neuronal processing is slowed down. If the interpretation of general slowing down holds true, we would expect an increase of all three factors, λ, N_A and t_o, which would then produce an increased T_A. If slowing down only affects sensory processing, depending on the extent and location of metabolic and electrophysiological changes, T_A would still be increased due to greater "delays along the sensory pathways" t_o.

A further hypothesis based on the claim of interhemispheric desynchronisation is that there will be no redundancy gain effect in the neglect group whereas an effect will emerge in the non-neglect and control group. This phenomenon refers to the fact that when targets appear in a bilateral visual field condition (the redundant target condition), the performance frequently improves compared to when the target is presented to only one hemisphere (e.g. Davis & Schmit, 1972; Mohr et al., 1994)

The second aim of this experiment was to analyse the response patterns in the subject groups. In Hellige et al.'s study (1989), vertical consonant-vowel-consonant nonsense syllables were presented tachistoscopically to normal subjects[8]. The CVC-stimulus was presented on each trial either to the left visual field, the right visual field or the same CVC sequence was presented bilaterally, i.e. simultaneously to the left and right visual field. Hellige et al. (1989) reported quantitatively and qualitatively different error patterns depending on the side of presentation of the CVC-non-word syllables. Fewer errors were produced when the stimuli were presented to the left hemisphere (38.8%) than the right hemisphere (61.3%) which was interpreted as a superiority effect of the left hemisphere for verbal processes. Hellige et al.'s results (1989) further suggested that the right hemisphere processed the CVC-stimulus as a set of three single letters, beginning with the top letter and proceeding serially to the bottom, whereas in the left hemisphere phonological mechanisms replaced or supplemented a single letter processing mechanism. Furthermore, the qualitative error pattern on bilateral presentation was similar to the left visual field presentation and different from the right field presentation which was a counterintuitive result, as the less appropriate hemisphere seemed to have taken over control. Also, although the qualitative nature of error patterns was similar on right hemisphere and bilateral trials, the error rate was much lower on bilateral trials.

In our study, we will only focus on the latter aspect of error pattern analysis, the redundancy gain effect. Our hypothesis is that a gain effect will not emerge in stroke patients with neglect as we have claimed that the two hemispheres are desynchronised. However, some gain effect is expected in the non-neglect group as the synchronisation of the hemispheres is only mildly impaired. The strongest effect is anticipated in the control group.

In summary, we will analyse the performance of a control group and two stroke patient groups with and without neglect in an inspection time paradigm. Slower reaction times to targets in the contralesional hemifield have been documented frequently in extinction or neglect patients (Làdavas, 1990; Behrmann & Meegan,

[8] Exposure duration was initially 200 ms. Following each correct response, this exposure duration was titrated downward by 10 ms until a duration of 150 ms was reached, after which titration was by 5 ms. Following each incorrect response, duration was titrated upward by 5, if below, or 10 ms, if above 150 ms.

1998). However, our special emphasis is focused on the performance of non-neglect stroke patients as we have hypothesised some impairment in the execution of the task due to general slowing down of neuronal processing (see also Duncan, 1998). The results will be analysed in the context of our temporal diplopia theory presented in chapter four. The experiment will examine the predictions of our hypothesis by establishing the inspection time needed to processes letter trigram stimulus correctly and by exploring potential redundancy gain effects. The stimuli will be presented in three visual field conditions: The left visual field condition (LVF), the right visual field condition (RVF) and the bilateral field condition (BIL).

2.2. Methodology

2.2.1. Inclusion/exclusion criteria and the neuropsychologcial assessment of subjects

The same criteria were applied as in the previous experiments (see chapter 5). Patients with all lesion sites were included in this experiment.

2.2.1.1. Intelligence

The National Adult Reading Test (Nelson, 1991; appendix 4) was performed with all the subjects participating in this experiment to obtain an approximate measure of their pre-morbid intelligence (Brody, 1992). It has been shown that performance in inspection time task is correlated with intelligence (Deary & Stough, 1996).

2.2.1.2. Visual field loss and visual acuity

The visual fields were assessed with the technique of confrontation as it is recommended by clinical medical textbooks. MacLeod and Monro (1986, p. 242) have described this technique as follows: The technique of confrontation "is based on a direct comparison of the patient's visual fields with those of the examiner as they look into each others eyes from a distance of about a metre. After an initial assessment made with both eyes open, the examiner shuts one eye and the patient covers the opposite" or the examiner covers the patient's opposite eye "so that the left visual field will correspond to the examiner's right and vice versa. The examiner

throughout the test, monitors the fixation of the patient's gaze since if the patient looks away from the examiner's eye the test is invalidated. The clinician then proceeds to test the outer limits by bringing a target into the field of vision from the periphery at several points on the circumference. The direction of approach should be distributed over upper and lower quadrants and nasal and temporal aspects of the visual fields. A satisfactory way to test each of the four quadrants is to advance the target towards the centre of gaze along lines at 45 degrees to the vertical and horizontal axes of the field. The test object should be moved on a plane mid-way between the patient and the examiner. A finger is a satisfactory target..." and was used in this study.

Visual acuity for near vision was tested with a standard reading chart recommended by the British Faculty of Opthalmologists (Hope et al., 1989, p. 33; appendix 5). Each eye of the patient is covered in turn and the patient is asked to read the smallest print possible at a distance of approximately 30cm from the eye. Glasses should be worn if required (MacLeod & Monro, 1986). If due to neglect dyslexia only parts of the word were read, the patient was still included as long as the letters of the non-neglected part of the word were identified correctly. A patient was included when words of the N. 12 category and below (N. 5, N. 8) could be read.

2.2.2. Subjects

Patients from the stroke rehabilitation unit from Drumchapel Hospital, Glasgow, participated in our study. Three neglect (average age 82 years) and three non-neglect (average age 74 years) stroke patients were examined[9]. The patients had suffered acute right hemisphere injury as demonstrated by CT-scan without any record of previous cerebral injury. Three healthy subjects (average age 74.6 years) were examined as control group. There was no previous illness in their past medical history of the control group (see tables 1 and 2 for patients' and subjects' profile). Mean average scores in the NART was 6 for the neglect group, 21 for the stroke patients without neglect and 16 for the control group. The differences of the mean age and the NART scores were not significant across the three groups. All subjects fulfilled the criteria set for visual acuity.

Table 1: Profile of patients and control subjects in study.

Patient/age/handedness/sex	CT-lesion	Time from cerebral injury at time of testing
Neglect Patients:		
1/79/R/F	R fronto-parietal infarct	2 weeks
2/85/R/F	R frontal lobe infarct	4 weeks
3/82/R/F	R parietal infarct	15 weeks
Non-neglect Patients:		
4/88/R/F	R temporo-parietal infarct	2 weeks
5/60/R/M	R deep temporal infarct	2 weeks
6/74/R/F	R deep fronto-temporal infarct	4 weeks
Control Subjects:		
7/66/R/F	-	-
8/72/R/M	-	-
9/86/R/F	-	-

Table 2: Patients' and control subjects' performance on star cancellation task, visual acuity test and National Adult Reading Test.

	Star cancellation tests 1 2 3 Side andnumber of stars cancelled			Visual acuity test	National Adult Reading Test (NART)
Neglect Pts.					
1	R/1	R/17	R/20	N.12	6
	L/0	L/0	L/0		
2	R/18	R/22	R/22	N.12	9
	L/4	L/4	L/4		
3	R/10	R/9	R/11	N.12	3
	L/0	L/0	L/0		
Non-Neglect Pts.					
4	R/27	R/27	R/27	N.12	33
	L/27	L/26	L/27		
5	R/27	R/27	R/27	N.8	15
	L/27	L/25	L/27		
6	R/27	R/27	R/27	N.12	15
	L/27	L/25	L/25		
Control Subjects					
7	Not tested			N.8	10
8	Not tested			N.12	5
9	Not tested			N.12	35

Note. Scores in the NART refer to the number of misread stimuli.

[9] Formal ethical approval had been obtained by the West Ethics Committee, Glasgow.

2.2.3. Apparatus

An apple MacIntosh computer LC 475 controlled all experimental events. It was stationed in one of the quiet hospital rooms. All the experiments were conducted in this room. The program with which the experiment was written was PsyScope 1.1.

2.2.4. Design

A mixed design was used. The between subject variable was cerebral damage with three levels (no cerebral damage, damage with unilateral neglect and cerebral damage without neglect). Two dependent variables were measured: The number of correctly reported letter trigrams and the number of errors contained in all responses. The within independent variables were inspection time with 12 levels (70 ms, 120 ms, 160 ms, 200 ms, 240 ms, 280 ms, 320 ms, 360 ms, 400 ms, 450 ms, 500 ms, 600 ms) and side of the visual field with three levels (LVF, RVF, BIL). All subjects were presented with the same stimuli and conditions.

2.2.5. Stimulus material and procedure

Stimuli consisted of a set of 36 CVC nonsense syllables (see appendix 3). The set of syllables was constructed by using the consonants D, F, G, K, P, S and T and the vowels A, E and O.

The CVC's were arranged vertically and appeared as black letters on a white background (see app. 8c for instructions to the subjects). The stimulus appeared either in the left visual field, the right visual field or the same stimulus was presented to both visual fields simultaneously. On LVF-RH and RVF-LH trials, the edge of the CVC nearest the centre was displaced approximately 5 degrees of visual angle from the centre. In the bilateral condition, the stimulus was presented simultaneously at the LVF- and RVF-locations simultaneously. Each CVC spanned approximately 2 degrees of visual angle horizontally and 4 degrees of visual angle vertically. An additional set of CVC stimuli was prepared in the same manner and used during a practice block.

Experimental trials were arranged in a set of 36 trials. There were 12 different stimulus durations (70 ms, 120 ms, 160 ms, 200 ms, 240 ms, 280 ms, 320 ms,

360 ms, 400 ms, 450 ms, 500 ms, 600 ms). The 36 CVC stimuli were presented randomly with the following restrictions: a) Each of the visual field conditions was presented 12 times; b) each of the stimulus durations would appear in every visual field condition (LVF, RVF, BIL). Similar restrictions were used to construct the 15 training trials.

A post-mask was constructed by using dollar signs. The mask appeared as a rectangle with its nearest edge approximately 5 degrees of visual angle from the centre and spanning 2 degrees of visual angle horizontally and 4 degrees of visual angle vertically.

A central fixation point, a cross, was presented which subtended approximately 1 degree of visual angle horizontally and vertically.

Each trial was initiated by the experimenter by pressing the appropriate button of the button box. The central fixation point appeared for 2 s and was followed by the CVC stimulus without delay. The stimulus was followed without delay by the post-mask presented to both visual fields for 500 ms.

Subjects were instructed to fixate their gaze on the central cross when it was presented and to identify the CVC stimulus first by pronouncing it and then by spelling it. The responses were transcribed by the examiner and recorded for further analysis.

In order to avoid invalid trials due to eye movements, a mirror was mounted on top of the computer. The experimenter was standing behind the subject and watching the eye movements. If eye movement occurred, the trial was marked appropriately. However, responses were included despite eye movement when the stimulus was presented for up to 160 ms, the approximate maximum time it takes to complete saccadic eye movement (Sadler & Deary, 1996; the above technique was adopted despite Jordan et al.'s recent findings that instructions to the subject to fixate centrally are insufficient, Jordan et al., 1998).

Each session included between one and three presentations of the stimulus set as described above depending on the patient's condition. In total, between 15 to 18 judgements were completed for each condition in between five and eight sessions. Each session took between ten and 20 minutes.

2.2.6. Results

Correct Responses

The correct responses were submitted to an analysis of variance. The main effect of Group reached significance (F (2, 6) = 8.39, $p < 0.05$). The neglect group (N) produced a mean number of correct responses of 5.79 compared with the non-neglect group (NN) of 8.85 and the control group (C) of 9.63 (see table 3). A post-hoc Bonferroni test established a significant difference between the control group and the neglect group (mean difference = 3.843, $p < 0.05$) and no significant difference between the control group and the non-neglect group (mean difference = 0.778, $p > 0.05$). However, the difference between the non-neglect group and neglect group only approached significance (mean difference = 3.065, $p = 0.064$). That is the non-neglect group did not produce significantly more correct responses.

Table 3: Mean number of correct responses in the three groups.

Neglect Group	Non-Neglect Group	Control Group
5.79	8.85	9.63

Furthermore, the main effect of visual field (LVF, RVF, BIL) reached significance (F (2, 12) = 69, $p < 0.01$). The mean correct responses were 5.61 for the LVF, 9. 32 for the RVF and 9.34 for BIL (table 4). In the post-hoc Bonferroni test, a significant difference emerged between the LVF and the RVF (mean difference = 3.7, $p < 0.05$) and between the LVF and BIL (mean difference = 3.73, $p < 0.05$). No significant difference was found between the RVF and BIL (mean difference = 0.028, $p > 0.05$), in other words there was no redundancy gain effect.

Table 4: Mean correct responses in visual field conditions.

LVF	RVF	BIL
5.61	9.32	9.34

There was also a main effect for Inspection Time (F (11, 66) = 32.7, $p < 0.001$). The mean number of correct responses at 70 ms was 4.85 and rose steadily to 10.6 at

600 ms (figure 3; see table 5). The post-hoc Bonferroni test performed multiple pairwise comparisons which are reported in table 6.

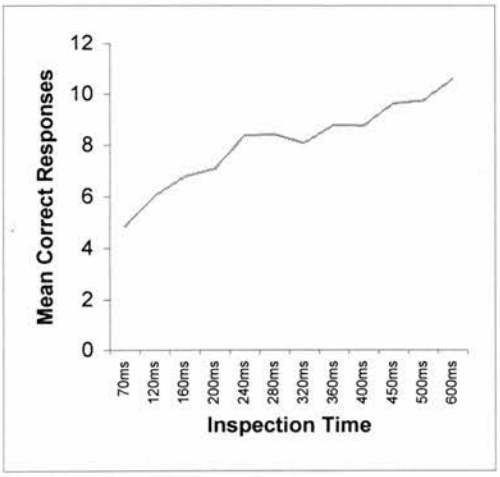

Fig.3: Collapsed mean correct responses.

Table 5: Mean correct responses at different inspection times.

70 ms	120ms	160ms	200ms	240ms	280ms	320ms	360ms	400ms	450ms	500ms	600ms
4.85	6.04	6.78	7.07	8.37	8.41	8.07	8.78	8.74	9.63	9.74	10.59

Table 6: Significance levels when mean correct responses are compared against each other at different inspection times (pairwise comparison).

	70ms	120ms	160ms	200ms	240ms	280ms	320ms	360ms	400ms	450ms	500ms	600ms
70ms	-	.8	.2	.065	**.005**	**.001**	**.028**	**.003**	**.014**	**.004**	**.004**	**.001**
120ms	0.8	-	1	1	**.002**	**.017**	0.2	**.007**	**.05**	**.003**	**.003**	**.001**
160ms	0.2	1	-	1	.6	.078	1	.2	1	.2	.17	.061
200ms	.065	1	1	-	1	.2	1	.4	1	.1	.1	**.043**
240ms	**.005**	**.002**	.6	1	-	1	1	1	1	.2	.1	**.004**
280ms	**.001**	**.017**	.078	.2	1	-	1	1	1	1	1	.1
320ms	**.028**	.2	1	1	1	1	-	1	1	**.015**	.9	**.01**
360ms	**.003**	**.007**	.2	.4	1	1	1	-	1	1	1	**.025**
400ms	**.014**	**.05**	1	1	1	1	1	1	-	1	1	.2
450ms	**.004**	**.003**	.3	.2	.3	1	.15	1	1	-	1	.2
500ms	**.004**	**.003**	.17	.12	.19	1	.9	1	1	1	-	1
600ms	**.001**	**.001**	.061	**.043**	**.004**	.1	**.01**	**.025**	.18	.24	1	-

A further significant source of variance emerged from the interaction between Group and Visual Field (F (4, 18) = 9.557, $p < 0.001$) as reported in table 7. The results show that for all groups the performance was worst in the LVF condition.

Table 7: Mean number of correct responses of groups in different visual field conditions.

	LVF	RVF	BIL
Neglect Group	1.47	7.89	8.0
Non-neglect Group	7.2	9.8	9.6
Control Group	8.2	10.3	10.4

In the neglect group, a non-parametric Friedman test revealed a difference that approached significance between the LVF and the RVF (χ^2 = 3, *d.f.* = 1, p = 0.08) and the LVF and BIL (χ^2 = 3, *d.f.* = 1, p = 0.08). There was no significant difference between the RVF and BIL (χ^2 = 0.3, *d.f.* = 1, $p > 0.05$). No significant results emerged in the other groups.

In summary, the performance of the neglect patients in the left visual field was worse than the performance in the right or bilateral visual field condition whereas no difference emerged between the right and the bilateral condition. No significant differences were recorded between visual field conditions in the other two groups. From this it also follows that in none of the three groups a redundancy-gain effect was discovered. In other words, the presentation of the same stimulus to both visual fields simultaneously did not influence the number of correctly reported stimuli neither in the neglect, non-neglect nor control group.

The interaction between Inspection Time, Visual Field and Group produced another significant source of variance (F (44, 275) = 2.2, $p < 0.01$). The mean of the correct responses for the different groups, visual field conditions and inspection times are represented graphically in figures 4, 5 and 6 a, b, c below.

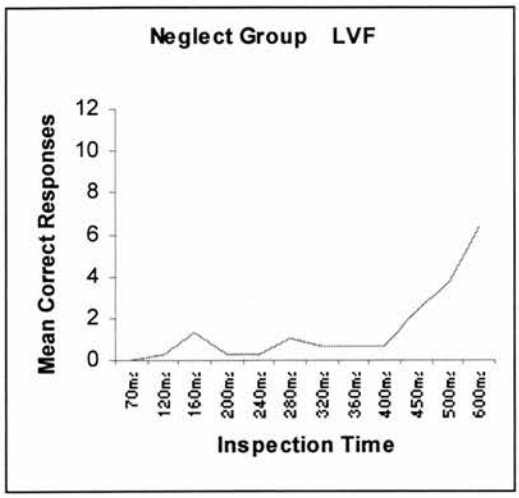

Fig. 4a: Correct Responses, Neglect group. Left visual field condition.

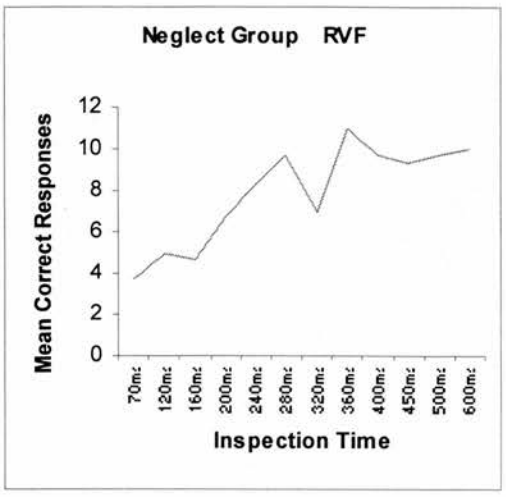

Fig. 4b: Correct Responses, Neglect group. Right visual field condition.

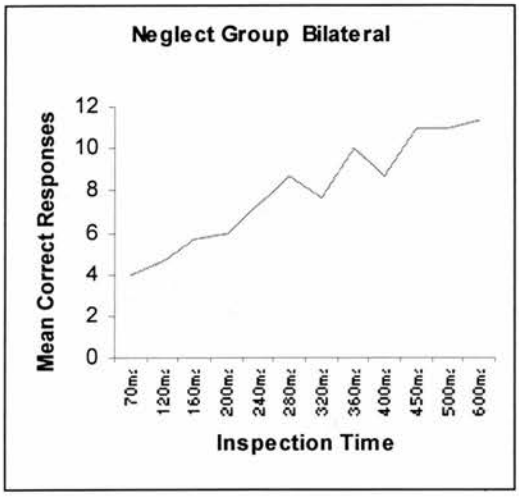

Fig. 4c: Correct Responses, Neglect group. Bilateral visual field condition.

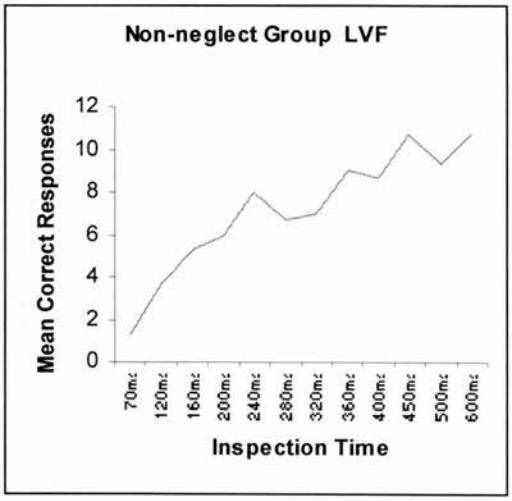

Fig. 5a: Correct Responses, Non-neglect group. Left visual field condition.

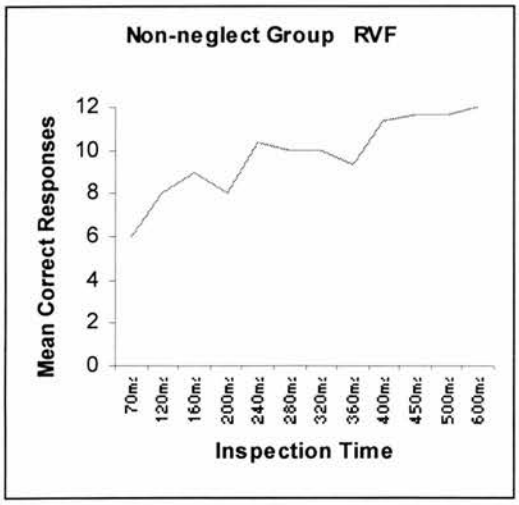

Fig. 5b: Correct Responses, Non-neglect group. Right visual field condition.

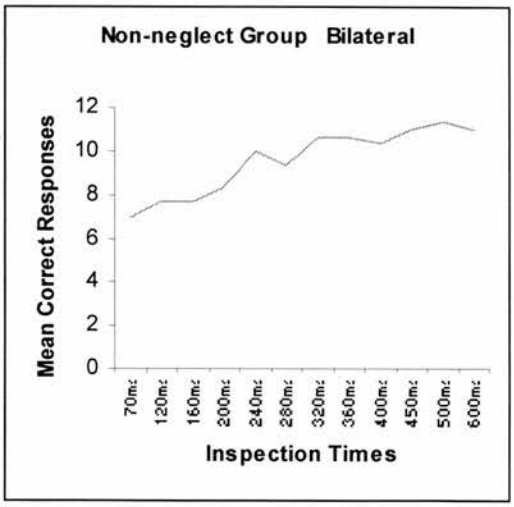

Fig. 5c: Correct Responses, Non-neglect group. Bilateral visual field condition.

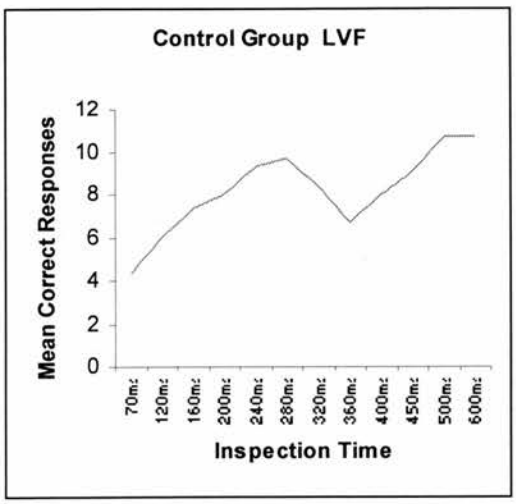

Fig. 6a: Correct Responses, Control group. Left visual field condition.

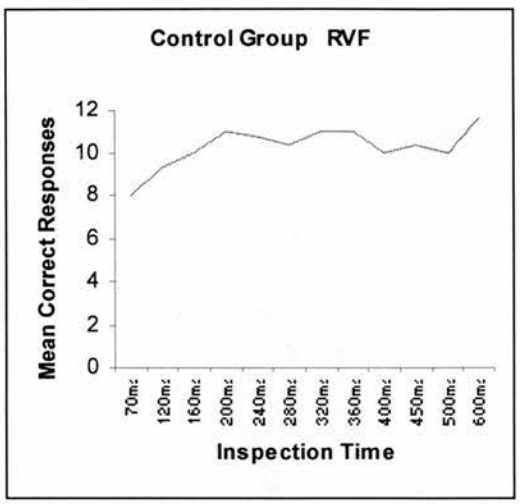

Fig. 6b: Correct Responses, Control group. Right visual field condition.

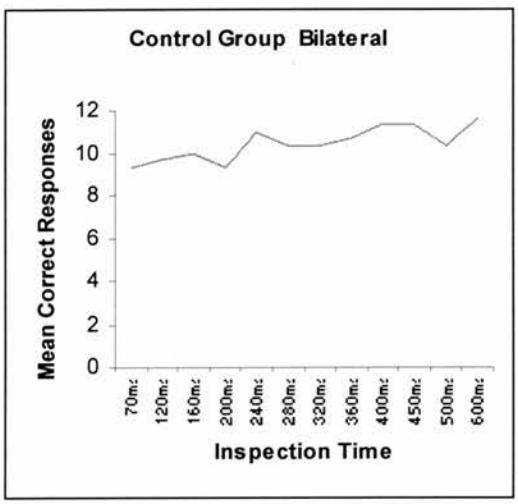

Fig. 6c: Correct Responses, Control group. Bilateral visual field condition.

A post-hoc Scheffé test was performed. No significant differences between the non-neglect group and the control group emerged for all visual field conditions and all inspection times. However, the neglect group produced significantly fewer correct responses compared to the control group and non-neglect group in the LVF as it is reported in table 8.

Table 8: Significance levels of smaller number of correct responses of neglect patients compared to non-neglect and control group in LVF (post-hoc Scheffé test).

Inspection Time	Control Group	Non-Neglect Group
70 ms	.09	0.7
120 ms	**.01**	.1
160 ms	.1	.3
200 ms	**.004**	**.01**
240 ms	**.003**	**.007**
280 ms	**.004**	**.03**
320 ms	**.004**	**.01**
360 ms	**.008**	**.001**
400 ms	**.05**	**.036**
450 ms	**.003**	**.001**
500 ms	**.015**	**.037**
600 ms	**.005**	**.005**

As for the RVF and bilateral visual field conditions, no differences were detected between the neglect group and the non-neglect group. Furthermore, the control group produced a higher number of correct responses only at an inspection of 120 ms in the RVF (mean difference = 4.3, $p < 0.05$) and at 240 ms in the bilateral field condition (mean difference = 3.67, $p < 0.02$) compared to the neglect group.

In short, the main significant difference lies in the performance of neglect patients in the LVF compared to the non-neglect group and the control group. Furthermore, in this condition the first significant results emerge at 120 ms for the control group and at 200 ms for the non-neglect group.

Error Types

The error types (first letter error, FLE; second letter error, SLE; last letter error, LLE) were analysed with regard to the redundancy gain effect and to qualitative differences in the error distribution. Figures 7a, b and c provide a graphical representation of the mean number of different error types in the different groups for all visual field conditions (see table 9a, b, c).

Table 9a: Mean number of error types in neglect group and all visual field conditions.

	LVF	RVF	BIL
FLE	0.05	0.17	0.17
SLE	1.86	1.19	1.33
LLE	0.64	1.06	0.72

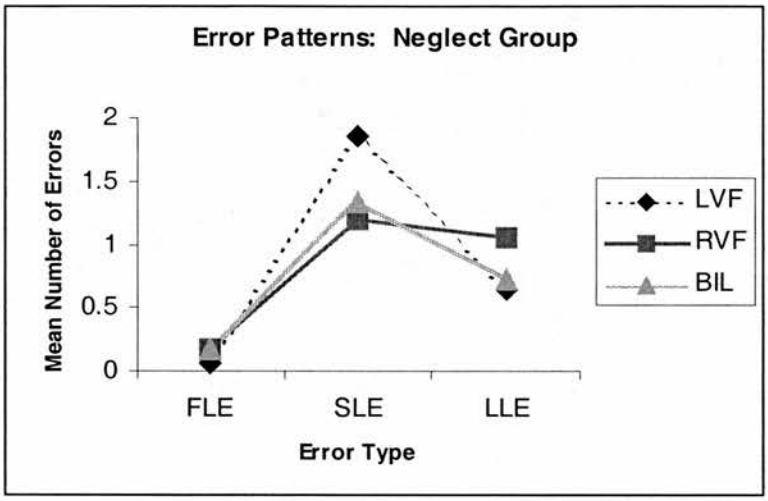

Fig. 7a: Mean number of type of error in neglect group.

Table 9b: Mean number of error types in non-neglect group and all visual field conditions.

	LVF	RVF	BIL
FLE	0.25	0.22	0.28
SLE	1.1	0.69	0.86
LLE	1.28	0.56	0.64

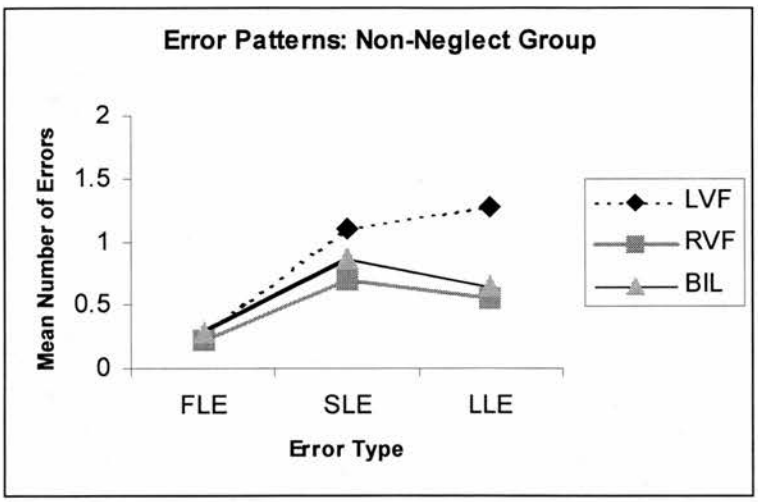

Fig. 7b: Mean number of error type in non-neglect group.

Table 9c: Mean number of error types in control group and all visual field conditions.

	LVF	RVF	BIL
FLE	0.139	0.11	0.083
SLE	1.528	1.167	0.917
LLE	1.11	0.22	0.25

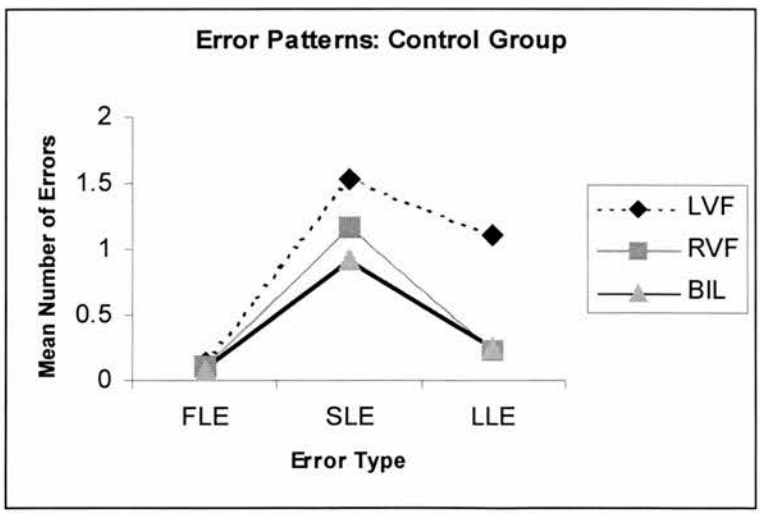

Fig. 7c: Mean number of type of error in control group.

A series of non-parametric Friedman tests was performed to investigate quantitative and qualitative error pattern distributions across groups and visual field conditions. The data showed, first, that a redundancy gain effect did not emerge either in the neglect group ($\chi^2 = 0.001$, $d.f. = 1$, $p > 0.05$), in the non-neglect group ($\chi^2 = 3$, $d.f. = 1$, $p > 0.05$) or in the control group ($\chi^2 = 0.3$, $d.f. = 1$, $p > 0.05$). In other words, the bilateral simultaneous presentation of a letter trigram did not reduce the number of errors committed by the different groups. Furthermore, figures 7a,b, c indicate qualitatively different error patterns for the LVF-RH compared to the RVF-LH/BIL visual field condition. More specifically, when the same stimulus was presented to both visual fields simultaneously the same distribution of errors was found as after presentation of the single stimulus to the RVF-LH. This effect did not only emerge in the two groups with right hemisphere damage but also in the normal control group. However, a series of non-parametric Friedman tests did not reveal any significant qualitative differences in the error distribution between the visual field conditions.

2.2.7. Discussion

To summarise our predictions, neglect patients were expected to require longer inspection times for targets in the left visual field than right hemisphere patients without neglect and the control group. Furthermore, it was predicted that in the LVF the non-neglect patients would display faster inspection times than neglect patients but longer ones than the control subjects. As for the redundancy gain effect, no effect of bilateral visual field presentation was expected to emerge in the neglect group due to interhemispheric desynchronisation but a moderate processing gain was predicted in the non-neglect stroke group and a stronger redundancy gain in the control group. Overall the neglect group produced the smallest number of correct responses which was significantly smaller than the number of correct responses produced by the normal control group. The non-neglect group, too, reported fewer correct responses than the control group but, contrary to the prediction, the difference was not significant. However, although the non-neglect group scored higher numbers of correct responses than the neglect group, the performance was not significantly

better. In other words, as anticipated, the non-neglect group showed some deficits in processing trigrams.

Unsurprisingly, the neglect patients required significantly longer inspection times for stimuli in the LVF than the non-neglect and control groups whereas performance in the RVF field was unexceptional compared to the other two groups. In contrast, the non-neglect stroke group did not perform significantly worse in the LVF when compared to the control group. However, a trend emerged, albeit tenuous, that might indicate a processing deficit of the non-neglect group in the contralesional visual field. While the control group was significantly more accurate than the neglect population at inspection times as short as 120 ms in the LVF, the non-neglect group required an inspection time of 200 ms to produce significantly more correct responses than the neglect patients. The observed impairment in the neglect and non-neglect group fit therefore with the hypothesis of slowed down neuronal processing in the damaged hemisphere.

The second important aspect of this investigation was the redundancy gain effect. Some tasks are performed better when the processing load is distributed across both hemispheres (Hellige, 1990). Such a between-hemisphere advantage is often revealed when the target is presented to each hemisphere simultaneously (redundant target condition) compared to single target presentation (Davis & Schmitt, 1971; Hellige et al., 1989; Eng & Hellige, 1994; Mohr et al., 1994; Minussi et al., 1998; Hasbrooke & Chiarello, 1998) and has even been documented in blindsight patients (Marzi et al., 1986; Corbetta et al., 1990b).

Two classes of models have sought to explain redundancy gain. The first account, the 'independent race model' (Raab, 1962), posited that each stimulus is processed by one of several parallel channels. A response is elicited as soon as a decision is made by one of the channels. A specific claim of the model is that information extracted from separate sources is kept strictly independent. The problem of information integration is therefore avoided by arguing that information is never pooled. The redundancy gain effect is accounted for by assuming probability summation or statistical facilitation. "If the distribution of finishing times for each of the two single targets overlap, then the mean finishing time of the winning decision process on

redundant target trials will be faster than either of the two single target means" (Mordkoff & Yantis, 1991, p.520). A second account was provided by the coactivation model (Miller, 1982). This approach claimed that signals from different channels and subsequent activation contribute to a common pool of activation that initiates a decision. That is, information from the two hemispheres is integrated and combined.

There has been increasing evidence in recent years that stimuli in the contralesional space which do not reach conscious awareness in the extinction or neglect patient undergo some degree of implicit processing (Volpe et al., 1979; Marshall & Halligan, 1988; Audet et al., 1991; Làdavas et al., 1993; Mijovic-Prelec et at., 1994; McGlinchey-Berroth et al., 1996; but see Behrmann & Meegan, 1998). Consequently, in extinction or neglect patients a redundancy gain effect might be expected on bilateral stimulus presentation even if the contralesional stimulus is not consciously perceived. Such an effect was demonstrated by Marzi et al. (1996). Three extinction patients following right hemisphere damaged were tested in a redundant target paradigm. The control groups were formed by two right hemisphere patients without extinction and three stroke patients with left hemisphere damage. The results revealed a redundancy gain effect in all three groups.

However, our study has proposed that in neglect patients the two hemispheres are desynchronised due to slowing down of the damaged hemisphere. Thus, it is irrelevant which of the above models of redundancy gain effect proves to be true. The slower the damaged hemisphere becomes, the less the distribution of finishing times for each of the two single targets will overlap in terms of the 'independent race model' or, in keeping with the framework of the coactivation model, the less information from the damaged hemisphere will be combined with the intact hemisphere. In either way, slowing down will be positively correlated with a decrease of the redundancy gain effect. Concordant with this interpretation, Marzi et al. (1996) reported that the amount of redundancy gain effect was less marked in the extinction patients compared to the right and left hemisphere patients. Unfortunately, no healthy subjects were examined in Marzi et al.'s study (1996).

In the current study, no redundancy gain effect was discovered - neither in the neglect group, as hypothesised, nor in the non-neglect group and control group of normal subjects. The failure to reveal an effect in the two non-neglect groups therefore renders the predicted absence of a gain effect in the neglect group meaningless.

The obtained results confirm the predictions made by the concept of 'metacontrol'. The term metacontrol was originally proposed by Levy and Trevarthen (1976, p.300) and refers "to the neural mechanisms that determine which hemisphere will attempt to control cognitive operations". In Levy and Trevarthen's study (1976), commissurotomised patients were examined for their ability to match stimuli that were presented simultaneously to both hemispheres. The results demonstrated that one hemisphere may frequently assert control over processing. This control appeared not so much to be dependent on the hemisphere's specialisation for a particular task but more on the expectations created before the execution of the task. The investigation of metacontrol in the normal brain requires a design such as that was used in this experiment, i.e. a design that produces qualitative hemispheric processing differences with unilateral presentations. Figures 7a-c illustrate qualitative differences in the error patterns. The LVF-RH condition produced more second and last letter errors than the RVF-LH condition. However, the differences did not prove to be significant. Furthermore, the qualitative error patterns of the bilateral visual field condition in figures 7a-c resemble the error patterns associated with the RVF-LH condition. From this one could infer that the mode of processing characteristic of the left hemisphere has dominated on bilateral trials (but see Hellige et al., 1989). A strict metacontrol interpretation would postulate complete left hemisphere control over the processing of bilaterally redundant stimuli, i.e. the qualitative and quantitative error distributions on bilateral trials would be identical to RVF-LH trials. Therefore, a bilateral gain effect, i.e. an improvement of the performance on bilateral stimulus presentation would be excluded. Consequently, our results are consistent with a metacontrol interpretation.

The above results are a replication of Mohr et al.'s findings (1994). In a redundant target paradigm, Mohr et al. (1994) presented function words, content words and pronounceable non-words tachistoscopically to healthy undergraduate students.

Analysis of the results revealed that bilateral presentation significantly improved both accuracy and reaction times of the subjects only in the word condition. No gain effect was reported for the non-words.

Before our final summary, one possible point of criticism should be addressed regarding the interpretation of our results. We have argued that in the above experiment the time for correct target processing was tested. Alternatively, one might say that we measured not the processing time but merely the time it takes to shift attention from the focus of attention to the target stimulus as the work of Làdavas and her colleague might suggest (Làdavas, 1990; Làdavas et al., 1990). In these studies, the authors claimed that both extinction patients and patients with neglect focus their attention on the right relative position. Therefore, the time to move attention across the right to a target in the LVF will necessarily produce longer inspection times. However, in the present study we will interpret our results within the framework of a prior entry phenomenon. In a temporal order judgement task, Rorden et al. (1997) examined two patients suffering from extinction after unilateral right parietal damage. The patient was sitting in front of a computer screen on which first a central cross appeared. This cross remained in place for the duration of the trial to provide a continuous central fixation point. Then a short horizontal line appeared on the left side, the side of extinction, followed by a second short horizontal line. The task of the patient was to indicate on which side the line first appeared. The results showed that the line on the left had to precede the one on the right by 200 ms to be perceived as appearing first. Rorden and his colleagues interpreted their results as "a genuine delay in visual awareness itself" (Rorden et al., 1997, p.429). Within the framework of our theory we attribute the increased inspection times to desynchronisation secondary to the slowed down processing of sensory information. In chapter four, we have illustrated that synchronised neuronal activity has been associated with consciousness and awareness (e.g. Singer, 1998). In so far, our view is in agreement with Rorden et al.'s interpretation of the data (1997). On the other hand, Làdavas' position remains untenable as long as no neurophysiological model of attention is put forward (Làdavas, 1990; Làdavas et al., 1990).

2.2.8. Conclusion

In the present study, three groups were examined: Right hemisphere stroke patients with and without neglect and normal control subjects. The processing of letter trigrams was investigated with regard to, first, the inspection times required for the target to be processed correctly in the left and right visual field and, second, with regard to a redundancy gain effect when the stimulus was presented in the bilateral field condition. The neglect patients required significantly longer inspection times compared with the other two groups to process the stimuli correctly in the LVF. The results are compatible with the predictions of our temporal diplopia theory and are interpreted as consistent with the claim of slowed down processing in the damaged hemisphere. Furthermore, there was some evidence for an impairment in the non-neglect group although it was only weak. First, the overall number of correct responses in the non-neglect group was not significantly better than the one of the neglect group which indicates some deficit. Second, in the LVF condition, the non-neglect group required longer inspection times than the control group to perform significantly better than the neglect patients. Taken together, the findings are compatible with the claim that both the neglect group and the non-neglect group process information in the damaged hemisphere more slowly. However, the findings regarding the redundancy gain effect are inconclusive. The absence of an effect in the neglect group, as it was predicted by our theory, cannot be used as evidence in favour of our theory as no gain effect emerged either in the non-neglect or the control group. The null hypothesis can therefore not fully be rejected.

Chapter Eight

Completion and subcortical processing of symmetrical stimuli in neglect dyslexia

1. Introduction

In a number of studies, it has been shown that neglect patients and patients suffering from neglect dyslexia can be sensitive to properties of the stimulus and the manner in which stimuli are presented to them.

For example, size (Tegnér & Levander, 1991; Halligan & Marshall, 1991b, 1993b, 1994, 1995; Marshall & Halligan, 1991, 1994) and symmetry (Driver et al., 1992; Ward et al., 1994) can influence the performance of neglect and extinction patients. Similarly, cueing can alter the perception of the stimuli in neglect patients (e.g. Riddoch & Humphreys, 1983; see Chapter 2, paragraph 3.2.2). As for stimulus properties of lexical stimuli, it has been shown that neglect dyslexic patients can respond to the configuration of a stimulus, e.g. symmetry (Shillcock et al., 1998) or lexical stimulus properties (Siéroff et al., 1988; Caramazza & Hillis, 1990; Riddoch et al., 1990; Brunn & Farah, 1991; Behrmann et al., 1990, 1994; Hillis & Caramazza, 1991).

In this chapter, we will first discuss some aspects of stimulus sensitivity in neglect and neglect dyslexic patients which is followed by a review of current theories of neglect dyslexia. Then we will present an introduction to the phenomenon of completion and discuss the relationship of completion with neglect dyslexia.

We have claimed that many aspects of unilateral neglect can be accounted for in a principled way by assuming desynchronisation of the hemispheres. In the last chapter, as predicted by our theory, no effect of bilateral gain was found. We will now investigate the question whether there will be differences in the performance of

neglect dyslexic patients when, first, the stimulus straddles both visual fields and, second, when the configuration of stimuli is symmetrical (Shillcock et al., 1998).

2. Some effects of stimulus properties

2.1. Size effects

Marshall and Halligan (1994) adopted the so-called "zoom-lens" model derived from the concept of an " 'attentional spotlight' with a variable beam diameter" (Marshall & Halligan, 1994, p.509) and combined the model with evidence on hemispheric differences in spatial processing. It was proposed (Marshall & Halligan, 1994; Halligan & Marshall, 1994) that the left hemisphere might preferentially reduce the diameter of the attentional spotlight and the right hemisphere might increase its size. Consequently, right hemisphere damage should shift the orientational bias towards the extreme right hemispace (Kinsbourne, 1987) with a focal processing mode of attentional distribution.

Based on these assumptions, it was predicted that a stimulus configuration which requires the allocation of panoramic/global attention should ameliorate neglect symptoms (see chapter 2, section 4.4.4., p.39, for a more detailed discussion of Halligan and Marshall's theory). The prediction was confirmed in several studies (Tegnér & Levander, 1991; Halligan & Marshall, 1991b, 1993b, 1994, 1995; Marshall & Halligan, 1991, 1994).

Tegnér and Levander (1991) examined 25 right hemisphere neglect patients in various bisection tasks. As predicted, long lines were bisected with a rightward error, and the patients displayed a cross-over effect in the bisection of short lines, short paper strips and small circles. By contrast, large circles and long white paper strips were bisected either accurately, or with leftward error. A similar result was reported in a single case study involving a right hemisphere neglect patient (Halligan & Marshall, 1993b). The patient was perfectly able to mark the four corners of a stimulus page in a line cancellation task. However, he kept omitting lines on the left hand side irrespective of whether his attention was drawn explicitly to the spatial dimensions of the stimulus sheet. In a different study (Halligan & Marshall, 1995), a modulatory effect of the stimulus sheet was indeed found. When horizontal lines were presented on differently shaped background sheets, the error decreased from

rectangle-shaped to a square- and circle-shaped background, respectively. In other studies (Halligan & Marshall, 1991b, 1994; Marshall & Halligan, 1991, 1994) it was demonstrated that accuracy in the bisection of squares and circles is far superior to the bisection of simple lines. Deviation decreased as the height of the figure increased. Furthermore, left neglect can be mitigated when the lines to be bisected form a square (Halligan & Marshall, 1994; Marshall & Halligan, 1994). The critical component for the accurate performance with squares seems to be a right vertical (Marshall & Halligan, 1994; Halligan & Marshall, 1994). The hypothesis that the patients might have used the estimated midpoint of a vertical to calculate the midpoint of the horizontal dimensions of the square was rejected on the grounds that no significant correlation was found between the vertical and horizontal displacements. It was therefore proposed that global attention processing was elicited by the configuration of the stimulus which "counteracts the (intact) left hemisphere's (intrinsic) tendency to orient rightwards with the subsequent 'capture' of focal attention by that part of the stimulus array which is in the extreme right position" (Halligan & Marshall, 1994, p.20).

It was further suggested that the global amelioration effect was mediated by the left intact hemisphere. The effectiveness of a vertical in the right hemispace might have prevented the left hemisphere from narrowing its 'zoom lens' (Halligan & Marshall, 1994).

However, Gainotti et al.'s (1986) findings are not concordant with Marshall and Halligan's model (1994; Halligan & Marshall, 1994). Gainotti et al. (1986) investigated to what extent the presence of neglect in right and left brain damaged patients could be influenced by different spatial tasks. Two tests were performed: An 'overlapping figures test' to investigate the deployment of attention to small but complex stimuli in the centre of the visual field. The second experiment was a 'searching for animals test': A large board with drawings of 20 different animals equally distributed to the left and right was placed in front of the patients. They were then given the figures of 40 animals one at the time. Twenty of these animals resembled the ones on the board, 20 did not. The patient's task was to identify the right animal on the board or to indicate that it was not present. Ninety patients with right hemisphere damage were tested. According to the scores of the overlapping

figures test, only 32 patients displayed signs of neglect whereas 37 patients were classified as suffering from neglect in the searching for animals test. According to Marshall and Halligan's predictions (1994; Halligan & Marshall, 1994), the search paradigm should have decreased the number of neglect patients.

2.2. Stimulus sensitivity in neglect dyslexia

Different patients are sensitive to different types of material. For example, Patterson and Wilson (1990) described a case where reading errors were mainly of the substitution type affecting the first letter only. Amongst other tasks, they tested the patient for a letter specific defect in his reading performance. For this purpose, Patterson and Wilson (1990) created a set of stimuli that consisted of a mixture of digits and lower-case letter strings. These were presented randomly to the patient, so that he could not know whether the stimulus started with a digit or a letter. The results showed that he was just as likely to misread a digit as a letter in the first position whereas he retained a striking ability to identify letters or numbers in the second position of the string.

Similarily, Riddoch et al. (1990) placed a hash sign (#) on the left end of letter strings to assess whether the # was coded as a member of the letter string. Their patient was told about the presence of the #, so it might function as a cue and thereby improve the performance of identifying the actual beginning of the letter string. The results revealed that, although the report of the initial letter in words and non-words improved, the patient made considerably more addition errors. In other words, the # was in some instances encoded as a letter.

Another example is Ellis et al.'s (1987) patient who made paralexic errors affecting mainly the leftmost letter. He also had problems reading sequences of numbers. Therefore, in all the cases mentioned above, the reading impairment was not specific for letters.

Furthermore, lexical constraints can be active in the processing of written material of neglect dyslexic patients, although some patients suffering from neglect dyslexia might not show any word superiority effects at all (e.g. Ellis, 1987). Others display a markedly better performance of words compared to non-words (e.g. Patterson & Wilson, 1990; Siéroff et al., 1988; Brunn & Farah, 1991; Behrmann et al., 1990,

1994; Caramazza & Hillis, 1990; Hillis & Caramazza, 1991; Riddoch et al., 1990). There are different theories as to why words can have a processing advantage. Caramazza and Hillis (1990) explained word superiority by the way in which lexical access is achieved for letter strings. A true word representation activates in parallel the associated lexical representations, some more and some less depending on the degree of how many graphemes are shared between the input word and the lexical representation. The lexical representation that is activated most will be produced as output. Since random letter strings have no lexical representation, they are much less likely to be produced as a response.

Riddoch et al. (1990) on the other hand attributed word superiority effects to top-down processes which are influenced by an interaction between attentional and lexical factors. These top-down processes endorse a more correct computation of the word length and the convenient viewing position (C.V.P.) and improve the deployment of attention. Similarly, Mozer and Behrmann (1990, 1992) proposed an interactive account following McClelland and Rumelhart's (1981) and Rumelhart and McClelland's (1982) ideas. According to Mozer and Behrmann (1990, 1992), top-down processes accelerate and influence the visual recognition of letter strings if two conditions are met. First, if a lexical representation exists that can be relayed "down" to complement lower level processing and second if the low level representation is not too degraded. If it is too disrupted the wrong lexical representation will be accessed, and no advantage will arise in the processing of this particular word. For the case of random letter strings, no lexical representations are stored and therefore either the wrong representation is activated or none at all.

Riddoch et al. (1990) further subdivided their stimulus material into high neighbourhood and low neighbourhood words. The degree of neighbourhood is determined by "the number of other words created by substituting one letter at any position in the word" (Riddoch et al., 1990, p.485). A significant effect of orthographic neighbourhood was found, i.e. a word with many orthographic neighbours was read much less accurately than a word with few orthographic neighbours.

A similar observation was reported by Patterson and Wilson (1990). Their patient, quite counterintuitively, was better at reading long words compared to short ones and

more successful at reading orthographically difficult words than common ones. After testing neighbourhood effects, they discovered that it was more important whether a word had neighbours than the size of the neighbourhood itself.

A further lexical constraint is word frequency. Hillis and Caramazza (1991) demonstrated that their patient read high-frequency words significantly better than low-frequency words. Equally, Riddoch et al.'s (1990) patient tended to do better with high-frequency words, albeit not significantly.

Configurational features of stimuli seem to influence processing of linguistic material, too. Shillcock et al. (1998) demonstrated that palindromic words, i.e. symmetrical linguistic material, had a processing advantage over non-palindromic words. However, before discussing this particular aspect of reading performance in neglect dyslexic patients, we will present an introduction to neglect dyslexia.

3. Neglect dyslexia

3.1. Introduction

Neglect dyslexia, caused by cerebral injury, most commonly by cerebro-vascular accidents, handicaps patients severely and very often prevents them from quickly resuming their lives after the experience of disability and hospitalisation.

In this section, we will provide a definition of neglect dyslexia, present a discussion of its clinical characteristics and the different theories of neglect dyslexia that have been put forward.

3.2. Characteristics of Neglect Dyslexia

3.2.1. Definitions and dissociations

Shallice and Warrington (1980) divided acquired dyslexias into two categories: Peripheral and central dyslexias. In central dyslexias, the word form is regarded as intact but the problem lies in the recognition and accessing of phonological and semantic knowledge. By contrast, the underlying deficit in peripheral dyslexias is the inability to create a visual word form (Shallice & Warrington, 1980). Apart from neglect dyslexia, they also assign spelling dyslexia (or letter by letter reading) and attentional dyslexia to the group of peripheral dyslexias.

Before addressing the issue as to whether neglect dyslexia is a syndrome independent of unilateral neglect, there are considerable problems in defining neglect dyslexia as an entity in itself. A variety of dissociations exist within neglect dyslexia depending on the reading task (single word versus text), the type of stimulus (number, letter, lexicality etc.) and frame of reference (viewer-, object- or environment-centred) (Behrmann, 1994).

3.2.2. Error patterns in neglect dyslexia

3.2.2.1. General error patterns

In neglect dyslexia, the patient displays a spatial bias for the processing of orthographic information in that he/she shows at least the following two symptoms: First, when given a text, the patient starts in the middle of a line, reads to the end of it and then focuses on the middle of the next line (e.g. Ellis et al., 1987). Second, the patient ignores the letters of a word contralaterally to his/her injury. That is, in the case of a right hemisphere injury, the beginning of a single word is neglected (e.g. Ellis et al., 1987; Riddoch et al., 1990). In the same vein, after left hemisphere damage, the patient commits paralexic errors that affect the end of the word (Warrington, 1991). Ellis et al. (1987) proposed the concept of a neglect point. For example, in the case of YELLOW → " PILLOW", the neglect point is between the e and the l in YELLOW. They classified "neglect errors operationally as errors in which the target and error words are identical to the right of an identifiable neglect point in each word, but share no letters in common to the left of the neglect point" (Ellis et al., 1987, p. 445). Obviously, this definition applies to left neglect.

The errors can be substitution errors where the length of the target and the response word are the same. Preservation of word length seems to be one of the characteristics of neglect dyslexia. Kinsbourne and Warrington (1962) first described this aspect in the behaviour of neglect patients. So, for example instead of SEAM, the patient would read TEAM, substituting the s for the t. These results have been replicated by several studies (Ellis et al., 1987; Behrmann et al., 1990; Patterson & Wilson, 1990; Riddoch et al., 1990; Warrington, 1991). However, this observation was confirmed by Tegnér and Levander (1993), too, but they also succeeded in inducing responses considerably shorter or longer than the target stimuli by varying lexical and

contextual parameters. Similarly, Chatterjee (1995) reported a patient who read 'lining' as 'sing', i.e. the first three letters were omitted and an additional letter was confabulated. Chatterjee (1995) referred to this type of response as commission error. Furthermore, omission and addition errors occur where the length of the response word does not correspond to the target word (Riddoch et al., 1990).

3.2.2.2. Single word versus text reading

Patients might have problems with both single word and text reading (Behrmann et al., 1990; Riddoch et al., 1990; Ellis et al., 1987; Kinsbourne & Warrington, 1962). Alternatively, they can do well in text reading producing errors only in the single word reading task (Costello & Warrington, 1987; Bisiach et al., 1986; Patterson & Wilson, 1990).

Young et al. (1991) proposed that different underlying processes cause these dissociations and posited a combination of different mechanisms when both single word and text errors occur. According to Young and his colleagues (1991), words are ignored on the left side of the page because of the defective location of the line beginnings. Deletions of initial letters of a word, on the other hand, are caused by the fact that the left part of the word falls into the hemianopic field of the patient with the patient habitually fixating on the middle or slightly to the left of the word depending on the word length (see O'Regan & Levy-Schoen, 1987). Young et al. (1991) blamed the lack of compensatory eye movements for single word deletion errors. Initial letter substitution errors, however, represent damage to mechanisms involved in letter and word recognition because they occur even when the entire word has been projected into the intact visual field.

This explanation appears a rather ad-hoc solution and is not supported by the data of Ellis et al. (1987) who pointed out that some neglect patients do not have any visual field defect at all (see also Albert, 1973). Conversely, patients with a homonymous hemianopia might not display neglect behaviour (Ishiai et al., 1987). To demonstrate that neglect dyslexic reading errors of their patient VB are not directly caused by a left homonymous hemianopia, Ellis et al. (1987) prepared stimulus cards on which a single red digit was placed 1cm to the left of a word that was printed in black letters. The patient was then asked to name the digit before reading the word. Thus, the word

must have fallen into the patient's intact right visual field. Despite this, the patient still committed 28 true neglect errors out of a stimulus set of 256 words. These errors included both substitution and omission errors. Nichelli et al. (1993) used the same technique as Ellis et al. (1987). The performance of the neglect dyslexic patient improved with the red digit to the left but did not abolish neglect behaviour completely. Therefore, the existing hemianopia cannot be the reason why compensatory eye movements are not applied as a strategy to overcome the handicap.

3.3. Theories of neglect dyslexia

Four theories will be presented that have attempted to describe the pathological mechanisms underlying neglect dyslexia: 1. A representational account (Caramazza & Hillis, 1990), 2. a length-constrained lexical activation model (Ellis et al., 1987), 3. an attentional model (Riddoch et al., 1990) and, finally, a connectionist model (Mozer & Behrmann, 1990, 1992; for a recent computational account see Anderson, 1999).

3.3.1. A representational account

The issue of representational frames leads us to the introduction of the first theory of neglect dyslexia. Caramazza and Hillis (1990) developed a multistage model of visual processing of orthographic material and postulated that neglect dyslexia can arise at any level with regard to different frames of reference. Their model was developed out of Marr's (1982) theory of visual object recognition. Marr (1982) postulated different levels and types of representation. The primal sketch provides an analysis of perceptual primitives like blobs and edges. The next step involves the creation of a 2 1/2-D sketch giving information about the object with regard to local surface, orientation and distance. Finally, there is the 3-D sketch which is an abstract, canonical representation of the object.

Caramazza and Hillis (1990) incorporated similar levels of representation of orthographic objects in their model. There are three stages of analysis: The retino-centric feature map, the stimulus-centred letter shape map and the word-centred grapheme description which is finally mapped onto a lexical orthographic

representation. Different computational requirements have to be met at each level of the recognition process. At the first level, the relevant features of the edges, blobs etc. have to be gained from the surface-reflected light intensities. This projection occurs with reference to the retinotopic frame. At the next stage, the existing description of step one is transformed into a representation where the letter shapes are only important in relation to each other and not, for example, into which part of the retina the leftmost letter has been projected. The last step creates a canonical representation of the orthographic stimulus which is independent of case, font and orientation of the single letters. This final representation is the word-centred grapheme description. For the word 'mouse' for example, the grapheme description is [<m>,<o>, <u>, <s>, <e>], no matter whether the stimulus looks like MOUSE, *mouse*, ***Mouse*** or MoUsE. Information about word length is implicitly encoded at the word-centred level.

Caramazza and Hillis' (1990) patient fitted snugly into this model. A deficit of the first level was excluded because the patient was able to name accurately all letters in a word but continued to misread it as a word. The second level, the stimulus-centred map, was ruled out as origin of the impairment because the patient made reading errors virtually only on the right half of words irrespective of the form of presentation (vertical, mirror-reversed or aural). A stimulus-centred map veridically represents the within-stimulus spatial relations, therefore, the stimulus-centred representations for vertical or mirror-reversed words are not the same. Since the patient produced a quantitatively and qualitatively similar performance irrespective of the form of presentation of the word, "there can be no single form of deficit" to the stimulus-centred map (Caramazza & Hillis, 1990, p.410). The authors interpreted these findings as clear evidence for a deficit in the word-centred grapheme representation.

Caramazza and Hillis (1990) then proceeded to review the existing neglect dyslexia literature and defined the deficit of the documented cases of neglect dyslexia with respect to their model. Accordingly, Kinsbourne and Warrington's (1962) patients were diagnosed as suffering from a deficit in the retino-centric map. On normal presentation of words, they showed left neglect but when the word was rotated clockwise by 90°, their reading improved instantaneously.

Evidence for defects at the stimulus-centred map comes from several studies. Ellis et al.'s (1987) patient continued to neglect the leftmost letter in a visual array. When words were presented in a normal fashion, the beginning of the word was ignored. When the patient had to read the same words, but this time mirror-reversed, the final letter of the word was affected. Similar reading behaviour was reported by Hillis and Caramazza (1991). Whether the words were presented in the normal or mirror-reversed orientation, the patient made errors on the left side of the physical stimulus. The same reading pattern was observed by Patterson and Wilson (1990) and Riddoch et al. (1990). However, both Riddoch et al. (1990) and Patterson and Wilson (1990) stressed to interpret these results with caution since exposure/reaction times were much longer for the mirror-reversed condition than the normal single word reading task.

In Caramazza and Hillis' (1990) theory, superior reading accuracy for words over non-words was not explained by top-down processes but different mechanisms of recognition and lexical access. Two assumptions must be made: "(1) ... a word-centred grapheme representation activates in parallel all lexical representations in proportion to the degree of grapheme overlap between the input and lexical representations; and (2) ... the lexical representation that receives the most activation, above a prespecified minimal level, or the one to reach threshold first, will be processed further and produced as a response" (Caramazza & Hillis,1990, p.427). Since there are no lexical representations for non-words, default correct responses will not occur.

However, the issue of the level of length coding remains unresolved. According to Caramazza and Hillis (1990) information of length is encoded implicitly at the word-centred grapheme description. They do not specify length coding at any lower level. This seems to be required, though, to explain addition errors induced by a # sign, for example, (Riddoch et al., 1990), a process that must have taken place on a level below the word-centred representation. Similarly, Caramazza and Hillis' model (1990) can not explain data obtained by Tegnér and Levander (1993) who induced much longer and shorter error responses compared to the target by manipulating lexical and contextual parameters. Sergent (1987) provided evidence for low level subcortical recognition of length. Two commissurotomised patients were presented

tachistoscopically with simultaneous bilateral information such that neither hemisphere received enough information to make a final decision. In a lexical decision task, two letters were projected to each hemisphere and formed either a four letter word or a four letter non-word. The patients were only able to report the letters projected to the right visual field. Although the subjects never succeeded in reporting the correct word, they tended to produce four letter words as response. Consequently, if there is indeed length coding at a level below the word-centred grapheme representation, Caramazza and Hillis (1990) have to modify their account which makes the model less attractive and less constrained. Another point of criticism is the fact that no mention is made of the classical laterality phenomenon in neglect dyslexia. More specifically, why do the majority of neglect dyslexia cases involve patients with right hemisphere lesions (Ellis et al., 1987)?

3.3.2. Length constrained lexical activation

Ellis et al. (1987) described a patient who displayed all the characteristics of neglect dyslexia. When reading single words, she consistently misread the initial letters. Substitution errors were her main error type whereas deletion and omission errors were in the minority. That is, the response word had the same length as the target word. It was interesting that no word superiority effect emerged. Words and non-words were misread alike. A different pattern emerged, when the patient read strings of numbers. There, deletion dominated her performance.

Ellis et al. (1987) proposed that the impairment causing neglect dyslexia occurs in the early visual processing system of letters in both words and non-words, excluding any top-down lexical processes or partial activation of existing lexical representations. According to this view, a "letter form analysis system " (Ellis et al., 1987, p.456) incorporates two subsystems that analyse the component letters with respect to letter identity and letter position. The authors referred to studies on iconic memory. Normal subjects first forget the position of a letter before they lose information as to which letter it was (Long, 1980). Also, migration errors which occur in normal subjects after brief tachistoscopic presentation of two words show positional coding processes. Having shown CONE and MAKE, the subject might report having read CAKE. The migration error, though, occurs only when the

transposed letter occupies the same position in the new word (Mozer, 1983). Ellis et al. (1987) interpreted these data as evidence for the two different subsystems.

Ellis et al. (1987) explained the preserved length responses and the lack of word superiority effect as follows: When the patient is shown the word MOUSE, her visual processing system might create an intact representation like M (1), O (2), U (3), S (4), E (5). In the case of impaired processing, the representation might look like - (1), O (2), U (3), S (4), E (5), and her error response might be HOUSE thereby filling the empty first positional place in the sequence. This kind of length-constrained lexical activation could also explain why the patient does not produce the response RAIN when presented the target word TRAIN but GRAIN, for example, or a confabulated word of the same length as the target. This is because the positional coding of the first letter is part of the representation.

According to Ellis et al. (1987), the fact that substitutions outnumbered deletions even when the error responses were non-words demonstrated that sublexical grapheme-phoneme conversion is based on the same positional coding mechanisms as for activating lexical representations. Ellis et al. (1987) explained occasional deletion and omission errors by pointing out that "positional encoding is naturally somewhat error prone" because "visual word recognition is an artificial, culturally transmitted skill which arguably requires more precise encoding of the left-to-right positions of elements within an array than any natural perceptual skill" (Ellis et al., 1987, p.458).

However, there are a number of critical points to be made at this point. The latter claim seems a rather far-fetched statement. It was not explained why any of the two subsystems should be more susceptible to malfunction than the other. Furthermore, Ellis et al. (1987) failed to mention the reported cases in the literature where lexical effects emerged. It might well be that Ellis et al.'s (1987) explanation could be applied to the patient they described in their study but this is not the case for the documented cases where patients showed clear word superiority effects (Patterson & Wilson, 1990; Siéroff et al., 1988; Caramazza & Hillis, 1990; Riddoch et al., 1990; Brunn & Farah, 1991; Behrmann et al., 1990, 1994; Hillis & Caramazza, 1991). Also, like Caramazza and Hillis' (1990) theory, Ellis et al.'s (1987) account was unable to explain much shorter and longer error responses provoked by changing

contextual and lexical environment (Tegnér & Levander, 1993). A further point is that Ellis et al. (1987) did not explain in their analysis why damage to one hemisphere should cause an impairment in the positional coding system contralaterally to the lesion. No explanation was given in Ellis et al.'s (1987) account as to why not also the internal positions or the ipsilesional positions of a word could be affected. Again, the problem of laterality phenomena is not incorporated in the model. Finally, the fact that deletion errors outnumbered substitution errors in number reading was addressed by the authors with the claim that the positional coding system of numbers is operated at a slower speed and with less efficiency and automaticity. Again, these claims are non-falsifiable and unsubstantiated arguments that allow the explanation of any reading disorder.

3.3.3. Length constrained attentional orientation to words

Like in Ellis et al.'s (1987) study, Riddoch et al.'s (1990) patient committed mainly substitution errors affecting the initial letters of the left half of the word. But unlike Ellis et al.'s patient (1987), he showed a word superiority effect and was more likely to produce real word errors than non-word errors which provides evidence for top-down processes. Furthermore, a # to the left of the word induced more addition errors. That is, length coding was susceptible to manipulations.

Riddoch et al. (1990) confirmed Ellis et al.'s (1987) suggestion that word length can be computed independently of letter identification but offered an alternative account how length information in conjunction with attentional processes could contribute to the impaired reading performance of neglect dyslexic patients. The authors argued that Ellis et al.'s (1987) theory was not supported by data from normal subjects. Humphreys et al. (1990) demonstrated in an orthographic priming paradigm that the length of the prime did not influence the actual priming effect of the target word. Riddoch et al. (1990), therefore, proposed that length information is used to control attentional orientation to words, in particular, to allocate the convenient viewing position for a word (C.V.P.) (O'Regan & Lévy-Schoen, 1987). O'Regan and Lévy-Schoen (1987) introduced the concept of the C.V.P. which is the position where the eye should fixate for visual recognition to be most rapid. The C.V.P. is near the centre and for longer words slightly left of the centre of the word. Riddoch et al.

(1990) argued that left neglect dyslexia could be caused by chronic orienting to the right of the C.V.P. The other factor which might determine what kind of error patterns will dominate is the correct or incorrect encoding of length information. If the length is computed correctly, substitution errors will occur. If the word length is overestimated, neglect dyslexic errors will decrease because attention is allocated further to the left or addition errors can be precipitated by adding a # to the left of the word, for example. Conversely, with underestimation of the word length, omission errors will dominate. Chatterjee (1995) proposed that word length errors are comparable with line bisection behaviour and that errors in both task can be expressed by a power function. Short words and lines tend to be extended. On the other hand, when the lines and words were longer, bisection right of the subjective centre and omission errors, respectively, occurred more frequently.

In summary, it is claimed that top-down processes are shaped by an interaction between attentional and lexical factors. The observed superiority effect, therefore, is caused by the top-down processes enhancing the computation of the C.V.P. and word length.

3.3.4. A connectionist model

Mozer and Behrmann (1990, 1992) proposed a connectionist model of neglect dyslexia which had parallels to the well known interactive activation model by McClelland and Rumelhart (McClelland & Rumelhart, 1981; Rumelhart & McClelland, 1982).

McClelland and Rumelhart's model offered a convincing alternative to early and late selection theories of visual processing. It demonstrated that in models of parallel processing the computations do not have to occur in a hierarchical successive manner. That is, early stages of processing can coexist with later stages of processing, and there is mutual interaction between the two levels.

In the literature, there was controversy as to whether attentional selection occurs early or at later stages of visual processing. Supporters of the early selection theory (Broadbent, 1958; Treisman, 1969) defended the view that a stimulus is selected before it is identified or any semantic information is accessed. Opponents of that

view (Deutsch & Deutsch, 1963; Shiffrin & Schneider, 1977) claimed that selection will not occur before the stimulus has been identified (see also chapter three, section 2.1., p.67). "According to the early selection view, disturbance of normal attentional functioning should result in the degradation or attenuation of low-level representation. According to the late selection view, the disturbance should come into play only after the stimulus has been processed to a high level" (Mozer & Behrmann, 1990, p.97)

However, there is evidence for both early and late selectional processes in the literature on neglect dyslexia. Hillis and Caramazza (1991) demonstrated that the error rate of their patient deteriorated with increased spacing between the letters of each word. This means that manipulation of low-level features which describe the sensory and physical properties of a stimulus had an effect on the processing of the orthographic material, and therefore suggested a deficit at an early stage. Similarly, Riddoch et al. (1990) tested to what extent contrast reduction would interfere with the performance of one of their neglect dyslexic patients. The degradation condition did not cause a significant deterioration of the patient's reading performance but the error pattern changed. Instead of mainly producing substitution errors, the patient increased the number of addition errors. This result suggested again that there are deficits in early visual processing.

By contrast, Làdavas et al. (1993) designed an associative priming task to test whether stimuli of which the neglect dyslexic patient was subjectively not aware would be processed for meaning at a deeper level. For this purpose, two sets of target and associated priming stimuli (words and non-words) were designed. The patient was required to focus on a fixation point. After a short interval, the priming word was presented to the neglected field. The duration of presentation was short enough to prevent the patient from fixating on the prime. Then the target word followed the prime and was projected into the intact visual field. The results showed that the responses of the neglect patient were significantly influenced by the prime stimulus presented to the neglected side. Làdavas et al. (1993) concluded that some post-perceptual processing of the neglected stimuli must have taken place. These results were confirmed by Berti et al. (1994) who performed a Stroop-like experiment. A neglect patient was asked to name the colour of target words. The results revealed

that naming times were affected by the prime stimuli presented to the neglected field, like in the experiment of Làdavas et al. (1993). Therefore, implicit reading must have processed the subjectively neglected material, albeit to a lesser extent than in normals.

"These paradoxical results rule out simple early and late selection views of attention. The early selection view cannot explain why selection may depend on higher order properties of the stimuli. The late selection view is contrary to the finding that neglect depends on the position and orientation of the word in the visual field" (Mozer & Behrmann, 1990, p.97).

Mozer and Behrmann (1990, 1992) addressed the above problems and designed a model in which the attentional deficit is located at an early stage. However, lexical effects can still arise at the same time if an interaction between high and low levels of processing occur. These top-down processes, therefore, influence the computation at a lower level. Top-down processes can help create a lexical representation despite degraded lexical information at a lower level but only on two conditions: First, if there are already existing lexical representations which can be fed down to complete the processing of the object; and second, only if the representation of the early stages is not too degraded to elicit activation of the corresponding word in the lexicon above threshold. These assumptions can account for early processing disruptions, lexical effects (word superiority, neighbourhood effects etc.) or the occurrence of both.

Mozer and Behrmann's (1990, 1992) connectionist model has been designed to incorporate these features of an interactive processing system. The model has been termed MORSEL, short for **M**ultiple **O**bject (word) **R**ecognition and **Sel**ective Attention. It consist of three different units: A connectionist network, the input side, which processes multiple letter strings in parallel. The capacities of this network are limited and processing errors increase with the amount of information that flows through the net. The second component is an attentional mechanism which acts as a spotlight to focus processing activity of the input network on certain letter strings. So, in metaphorical terms, the network creates a kind of retinal feature map when processing letter strings which then are focused upon for preferential processing by the attentional mechanism, thereby gating the flow of activity through the network.

The third component of the model is the so-called pull-out network that generates an interpretation from the noisy output of the network. The selection process of the pull-out network is influenced both by bottom-up information flow and top-down information from semantic lexical units which provide stored information on lexical entries. Apart from the pull-out net, the attentional mechanism, too, receives bottom-up (from the input net) and top-down information from "higher levels of cognition" (Behrmann, 1994, p.193).

According to Behrmann (1994), three properties of the net are essential to explain some of the data of neglect dyslexia when damaged. Attentional selection occurs at an early processing stage. Furthermore, even unattended information is analysed partially. And last, noise and degraded representations can be compensated for by stored long-term information through top-down processes.

To test the relevance of the model for neglect dyslexic errors, Mozer and Behrmann (1990, 1992) damaged the attentional mechanism in the model involving the bottom-up connections from the input network. The lesions were instantiated in a particular way to implement an attentional gradient from left to right which Mozer and Behrmann (1990, 1992) regarded as the underlying deficit in neglect. In fact, many of the patterns observed in neglect dyslexia were successfully simulated.

In summary, the model offers a unified account of apparently contradicting data in neglect dyslexia by proposing a system of interactions between degraded perceptual input caused by an attentional deficit and top-down processes. The model is also more suitable to explain the data obtained by Tegnér and Levander (1993). Tegnér and Levander (1993) induced responses much shorter or longer than the target stimulus. Manipulation of contextual parameters produced a much longer response, for example MINSKA SJUKHUSET ('reduce the hospital') → KAROLINSKA SJUKHUSET ('Karolinska hospital'). Also, modifying the lexical parameters often led to much shorter responses. Words with a free-standing right morpheme, compound (SOLROSE, sunflower) or embedded (NEUROS, neurosis), were often shortened to the free-standing morpheme, i.e. ROS in this case. Neither of the above mentioned theories of neglect dyslexia can deal with these phenomena, whereas Mozer and Behrmann (1990, 1992) can account for the data more convincingly. They assumed an attentional gradient which in the case of MINSKA SJUKHUSET

for example focuses mainly on the right side of the string of letters, depending on the slope of the attentional gradient, with the left side still being implicitly processed. The pull-out mechanism then constructs the most plausible interpretation and produces KAROLINSKA SJUKHUSET, an already stored lexical representation.
The connectionist concept appears more coherent than the other theories discussed above. A weak point, though, is the way the lesions were built into the model. If lesions are implemented with a gradient from left to right, one would expect the production of output responses with a gradient of accuracy from left to right, too.
In the next section, we will turn to the question of how neglect dyslexia ties in with the phenomenon of unilateral neglect.

3.4. Neglect dyslexia: A reading specific deficit?

In this section, we will present evidence for and against the view that neglect dyslexia is an impairment independent of unilateral neglect. Caramazza and Hillis (1990), for example, adopted and modified Marr's (1982) model of visual object recognition to describe the processes involved in visual word recognition as discussed in detail above. The authors developed a hierarchical system of processing levels for words which are analogous to Marr's (1982) level of object recognition. No clear distinction is made between the computation of objects and letter strings. The question is not discussed in what way visual recognition of orthographic objects is different from visual recognition of a chair, for example, or whether there is a difference at all. The computational requirements are the same in both instances apart from the step of mapping the word-centred grapheme description onto a lexical orthographic representation as compared to the mapping of an abstract canonical representation of a chair onto a stored visual or also a lexical representation of a chair. "We take it that this process" (the mapping of a grapheme description on a lexical orthographic representation) "is not dissimilar in its general form to that involved in visual object recognition" (Caramazza & Hillis, 1990, p.392).
Ellis et al. (1987) were more explicit in these questions. They rejected categorically "that there is anything about 'neglect dyslexia' that is specific to reading. The symptoms occur because visual neglect happens to compromise the reading process" (Ellis et al., 1987, p.460). Their patient treated words and non-words alike,

displaying no lexical effects which prompted Ellis et al. (1987) to conclude that the deficit is caused by a disruption at the early stages of a general visual processing system. They even went as far as to say that they "do not anticipate the discovery of patients who show neglect dyslexic symptoms in the absence of any other features of visual neglect" (Ellis et al., 1987, p.460).

This last prediction was challenged by Costello and Warrington (1987). Costello and Warrington (1987) stressed that for example Kinsbourne and Warrington (1962) only found a loose correlation between neglect dyslexia and unilateral neglect. In the same vein, they pointed out that most studies analysing data on neglect patients imply that single word reading in these patients remained unimpaired. In addition, a strong piece of evidence for a dissociation of unilateral neglect and neglect dyslexia was presented in their study (Costello & Warrington, 1987). The patient described by Costello and Warrington (1987) had suffered a left hemisphere lesion which extended into the right hemisphere caused by a tumour. Interestingly, he showed symptoms of left neglect dyslexia but right visuo-spatial neglect in the line bisection and the figure copying task. Costello and Warrington's (1987) argued that, if Ellis et al. (1987) were right, the patient would either suffer from left neglect dyslexia and left visuo-spatial neglect or right dyslexia with right visuo-spatial neglect. The data of Costello and Warrington (1987), however, were not reconcilable with Ellis et al.'s (1987) prediction and have therefore suggested two different underlying deficits for neglect dyslexia and unilateral neglect.

An unusual case was presented by Warrington (1991) in that their patient showed symptoms of a right-sided neglect dyslexia. After analysis of the error pattern, Warrington (1991) stressed the symmetry between this case of right neglect dyslexia and the commonly described performance of patients suffering from left neglect dyslexia. Furthermore, Warrington's (1991) patient did not show any signs of right visuo-spatial neglect. The similarities between left and right neglect dyslexia and the absence of any visuo-spatial symptoms prompted Warrington (1991) to regard "both left and right neglect as highly selective deficits" (Warrington, 1991, p.203)

Riddoch et al. (1990) has also advocated the idea of a reading specific impairment. Two patients with right hemisphere damage were investigated in their study. Both

patients displayed left neglect dyslexia but only one patient showed signs of left neglect. Furthermore, the patient without signs of unilateral neglect omitted the left side of words only on very brief presentation of the stimuli. However, after detailed investigations, Riddoch et al. (1990) arrived at the conclusion that although the deficit in the patients was quantitatively different, they nevertheless qualitatively suffered from the same impairment that caused neglect dyslexia. Riddoch et al. (1990) who combined Caramazza and Hillis' (1990) representational multi-stage model with an attentional account considered the exaggerated attentional orienting to the right side of the words as a possible factor causing a reading specific impairment. Overall, the data on these questions are inconclusive. Caramazza and Hillis (1990) have not specified the problem explicitly, and Ellis et al.'s extreme prediction (1987) has been proven wrong by subsequent studies. Other studies have subscribed to the concept of neglect dyslexia as a reading specific disorder (Costello & Warrington, 1987; Riddoch et al., 1990; Warrington, 1991).

As for Costello and Warrington's (1987) patient, the described dissociation can only be accepted with certain restrictions. The clinical tests commonly used to identify these disorders are not very reliable and sensitive (Halligan et al., 1989). In particular, the tests used by Costello and Warrington (1987), the line bisection and a copying task were discarded by Halligan et al. (1989) as a relatively useless diagnostic tool. Therefore, it is theoretically possible that Costello and Warrington's (1987) patient whose cerebral lesions involved both hemispheres could have had unilateral neglect on the left in addition to right-sided neglect if a star cancellation task had been performed, a test recommended by Halligan et al. (1989) for its sensitivity. Equally, short exposure times of words presented on a screen might have revealed right-sided neglect dyslexia in conjunction with a more pronounced neglect dyslexia on the left side.

In summary, the whole discussion about the specificity of the impairment will remain unsatisfactory until more reliable standardised methods for tests and classifications have been introduced.

4. Processing of symmetrical linguistic material in neglect dyslexia

4.1. Introduction

The line bisection task is a simple but still very commonly used test in clinical and experimental studies of neglect. Patients with left neglect typically bisect horizontal lines right of their objective midpoint. However, Bisiach et al. (1983) were the first to provide data on the counterintuitive phenomenon of the so-called 'cross-over effect': The right displacement of the midpoint becomes increasingly smaller for lines with decreasing length. Finally, the neglect patient marks the midpoint *left* of the objective centre of the shortest lines. Later Halligan and Marshall (1988) replicated the cross-over effect in a study involving two left neglect patients. As one of their many theories (Marshall & Halligan, 1989; Halligan & Marshall, 1989; Halligan et al., 1990; Marshall & Halligan, 1990; Halligan & Marshall, 1991; Halligan & Marshall, 1993), Halligan and Marshall (1988) postulated an attentional boundary situated to the left of the true midpoint of the horizontal line to explain the patients' performance in the horizontal line bisection task. According to this theory, the neglect patient subjectively perceives the line only to the right of the attentional boundary. Small lines, however, do not extend to this boundary. Halligan and Marshall (1988) hypothesised that short lines are completed to this boundary. The patient "thus bisects (on some trials) a space that is devoid of sensory information but is filled in by an 'internally represented' line" (Halligan & Marshall, 1988, p.327).

Ishiai et al. (1989) postulated the involvement of completion phenomena in the incorrect bisection of long lines without commenting on the inaccurate bisection of short lines. They investigated the eye-fixation patterns of 21 hemianopic patients with left neglect in a line bisection task. The lines were 15 and 20 cm long. The results showed that the patients scanned the right part of the line, fixated on a certain point which was the leftmost point of the line explored by eye movements and marked this point as the subjective centre of the line. No leftward searches and only a few rightward searches occurred. Ishiai et al. (1989) suggested that the patients perceive a line which extends equally to both sides with reference to their fixation point. "The right hemisphere completes the line, using the visual input relating to the right part of the line perceived by the left hemisphere" (Ishiai et al., 1989, p.1485).

Based on this hypothesis, the configuration of the stimulus perceived by the left hemisphere might influence the completion processes in the right hemisphere. A second conjecture would be that interhemispheric processing might be facilitated by mirror-symmetrical stimuli and that completion phenomena should occur more frequently with symmetrical stimuli than non-symmetrical stimuli. In the next section, we will present a short review of completion phenomena to explore these predictions.

4.2. Completion

"Perceptual completion is the process of filling in the missing information when part of a figure falls in a blind area of vision. It implies the capacity to see more than is objectively available and suggests that the emerging percept is not a one-to-one mapping of the pattern of stimulation within the retinotopically organized visual cortex" (Sergent, 1988, p.347). It should be stressed at this point that perceptual completion does not apply to the ability to identify an object despite missing parts or a degraded representation (for a review on the limitations of the visual system see Kulikowski et al., 1991).

In a review of perceptual completion, Sergent (1988) discussed both physiological and patho-physiological conditions under which perceptual completion can occur: The blind spot, completion in commissurotomised patients and completion in hemianopic subjects.

The so-called blind spot, the site where the visual nerve merges with the retina, is a blind area in the visual field situated temporally to fixation. When both eyes receive visual input, the loss of information from the blind spot is compensated for by the corresponding sensitive area of the other eye. The deficit only becomes apparent in monocular vision. However, the blind area is not perceived as a "hole or as a dark spot, but looks homogenous with its immediate surroundings which seem to 'invade' the blind area" (Sergent, 1988, 349).

A second area of research where completion phenomena have been investigated are studies with commissurotomised patients (e.g. Levy et al., 1972; Sergent, 1988). After section of the forebrain commissures, each hemisphere receives information

only from one visual field due to the contralateral projection in the visual system. Visual information has been shown to be exchanged at a subcortical level (Trevarthen & Sperry, 1973; Holtzman, 1984; Sergent, 1986, 1987), but subcortical information has been described as mainly contextual and associative (Myers & Sperry, 1985). Levy et al. (1972) demonstrated that patients with anterior commissures disconnection perceived a half face as complete when it was projected into the hemisphere that controlled the response. Sergent (1988) replicated Levy et al.'s (1972) findings but also reported that the patients only completed a half face when another half face was projected to the other visual field. Since the patients were commissurotomised, Sergent (1988) suggested hemispheric interaction on a subcortical level.

A second patient group in which completion phenomena have been reported in the past are subjects with hemianopic visual field loss (e.g. Poppelreuter, 1917; Bender & Teuber, 1946; Pollack et al., 1957; Warrington, 1962, 1965; Gassel & Williams, 1963; Torjussen, 1978; Weiskrantz, 1990; Marcel, 1998). The site of cerebral damage leading to the visual field loss is not specified in the older studies. However, Torjussen (1978, p. 16) only included patients with a "hemianopsia of postgeniculate origin" in the study, while the patients of Weiskrantz (1990) and Marcel (1998) had suffered lesions to the striate cortex. The lesion site has implications for the remaining visual function. Destruction or denervation of the striate cortex produces a scotoma in the corresponding part of the visual field but studies have demonstrated that some patients possess a preserved ability to detect and discriminate stimuli presented within the blind area of their visual field although the patients deny seeing anything (Pöppel et al., 1973; Weiskrantz et al., 1974). This phenomenon is commonly referred to as 'blindsight' (for a review see Weiskrantz, 1990). Research in monkeys and in brain damaged human subjects has suggested that the remaining visual sensitivity is mediated by projections to subcortical structures like the superior colliculus, the lateral geniculate nucleus, the pulvinar nucleus and the extrastriate cortex (King et al., 1996; Stoerig & Cowey, 1997).

Poppelreuter (1917; quoted by Sergent) was the first to present half figures tachistoscopically into the intact and impaired visual fields. He termed the observed completion behaviour "vorstellungsmässige Ergänzung" (imaginative completion) of familiar figures and compared it to the physiological completion processes of the blind spot. Poppelreuter's (1917) approach to explain his results was empirical in that he believed sensory completion not to be different from normal perception. According to Poppelreuter (1917), the filling in of missing parts is just as in normal perception based on expectations and previous experience. He regarded the hemianopic visual field as an extended blind spot (see also Gassel & Williams, 1963).

Fuchs (1921; quoted by Gassel & Williams, 1963) tested three hemianopic patients tachistoscopically by presenting them simple figures like a circle or a square, familiar figures like a dog or bottle and complex ones like letters or words. Only the simple, symmetrical forms were completed by the patients. Fuchs (1921) interpreted his results within the framework of Gestalt theory which defines completion as the product of autonomous forces that create symmetrical and regular configurations. Three questions are particularly relevant in the context of our study: Are symmetrical figures completed more readily? Second, could this completion behaviour be based on hemispheric interaction? In other words, was completion in objectively complete figures (half of the figure is projected to the damaged and the other half to the intact visual field) observed more frequently than in objectively incomplete ones (only one half of the figure is projected into the intact visual field whereas the damaged visual field is not presented with a stimulus). And third, is neglect associated with completion? All studies mentioned here used tachistoscopic presentation of the stimulus material with two exceptions. Gassel and Williams (1963) used cards that were introduced into the visual field in a confrontation position, and Torjussen (1978) tested his subjects by using prolonged flash-induced afterimages.

As for the question of stimulus sensitivity in hemianopic patients, some studies reported that *only* symmetrical figures were perceived as complete (Poppelreuter, 1917; Fuchs, 1921; Torjussen, 1979). Other researchers documented that completion was present both in symmetrical and complex forms (Bender & Teuber, 1946, quoted

by Gassel & Williams, 1963; Warrington, 1960, 1965). Warrington (1960, 1965) demonstrated completion in both stimulus categories. In the earlier study (1960), completion of non-symmetrical stimuli in hemianopic patients was reported to be as strong as of symmetrical stimuli. Later Warrington (1965) found that the highest incidence of completion responses was associated with symmetrical geometrical shapes. The results showed a completion response to geometrical figures in 49% compared to 36% for complex figures. Marcel (1998) found a strong symmetry effect in his two hemianopic patients. However, it was also reported that sometimes the patients perceived accurately the blind field stimuli which were not mirror-symmetrical as long as the two halves of the figure fell on areas of symmetrical retinal eccentricity.

Our second and third questions to be addressed were whether completion was influenced by unilateral or bilateral presentation of the stimulus and whether there is an association with neglect.

Poppelreuter's (1917) patients reported complete figures even when an objectively incomplete form was presented with the missing part being projected into the blind hemifield. Similarly, Fuchs (1921) emphasised that the truly incomplete figures were perceived as whole ones. In a different study, Pollack et al. (1957) confirmed Poppelreuter's (1917) and Fuchs's (1921) results. Pollack et al. (1957) found completion to be independent of the objective completeness of the stimulus. Ten hemianopic patients out of 23 persistently reported a complete figure. Only when the missing parts and gaps of the stimulus where projected into the intact hemifield, the patients made reports of an incomplete stimulus. However, eight out of these ten patients were confused. Furthermore, eight out of these patients suffered from unilateral neglect. As Pollack et al. (1957, p.226) pointed out, the fact that only full or incomplete circles were used had "some influence in 'setting' these patients to report full circles". Also, a characteristic behavioural pattern in neglect patients is perseverance. It is conceivable that in this case, throughout the experiment the patients adhered to one answer with which the examiners seemed to be content.

Bender and Teuber (1946) on the other hand claimed that only objectively intact forms were completed with each half of the stimulus being projected to each visual

hemifield. Warrington (1962) pointed out that evidence for this claim was relatively weak since only one patient was investigated with only one incomplete figure. However, Warrington's results (1962) revealed a stronger tendency to complete an objectively complete object compared to objectively incomplete forms. Those patients who subjectively completed 60% or more of half figures showed 90 to 100% of completion for objectively complete figures. Similarly, subjects who showed only 0 to 30% completion for the half figures, reported 0 to 50% of objectively complete figures as complete. A clear cut result regarding unilateral versus bilateral presentation in connection with completion was provided by Torjussen (1978) who reported completion phenomena exclusively for objectively complete symmetrical stimuli. Three hemianopic patients were investigated. When only one half of the figure was presented to the intact field, no completion was reported. Torjussen (1978) made no reference to mental state, awareness of the field defect or neglect. The same result was obtained by Marcel (1998). Only objectively complete figures were completed by the hemianopic patients.

As in Pollack et al.'s study (1957), Warrington (1962) revealed an association of neglect with completion. Out of the eight neglect patients, seven showed completion behaviour, a result that did not reach significance levels, though. Warrington (1962) also demonstrated a significant relationship between unawareness of visual field defects and completion. All patients who lacked insight into their field defects exhibited completion. On the other hand, deterioration of the patients' mental state did not prove to be relevant.

Sergent (1988) examined six hemianopic patients and did not find any signs of completion in four of them. In the fifth patient, completion responses were given both to objectively complete and incomplete figures only after her clinical and mental state had deteriorated. As for the sixth patient who was known to possess residual vision on his affected side, 80% of his completion responses occurred after the presentation of an objectively complete stimulus and 20% after an incomplete stimulus. The last two patients who showed some completion effects suffered both from unawareness of the visual field defect and visual neglect. Out of the four patients without completion, two were aware of their visual field loss and had no

neglect, and the remaining two patients suffered both from neglect and unawareness of their visual field loss.

In a study by Warrington, (1965) only incomplete figures were used and there was no reference to neglect in the hemianopic patient group. Gassel and Williams (1963) did not break up their results with respect to unilateral and bilateral presentation of the stimuli. A group of 35 hemianopic patients was examined and the results showed a high level of completion in seven patients, a moderate tendency to complete in 13 patients, a low tendency in ten patients and little to no tendency to complete in five patients. Gassel and Williams (1963) also reported that a low level of insight into the visual field defect appeared to be associated with a high tendency for completion and vice versa. As for the relationship between neglect and completion, it was stated that completion "was most resistant to demonstration in those patients with some complicating feature in whom direction of attention would be expected to be unsuccessful... " (Gassel & Williams, 1963, p.255).

Sergent (1988) discussed a number of reasons that might erroneously produce a completion response in a patient. First, it has to be ascertained that the patient clearly understands the requirements of the experimental task. In a number of studies, mental deterioration was reported to be associated with completion (Pollack et al., 1957; Warrington, 1962; Gassel & Williams, 1963; Sergent, 1988). Consequently, to test the hypothesis that perceptual completion is a genuine phenomenon, cognitively impaired patients should be excluded. Second, the type of response the patient is asked to produce might distort the results. In most of the studies, a verbal response was given by the patient. The translation of the physical contents of the percept into a linguistic representation might exhaust the processing capacities of the patient. To avoid this problem, Sergent (1988) asked her patients in the study to draw a picture of what they have seen. However, one of the classic behavioural patterns of neglect patients is to omit the neglected side in their drawings. Theoretically, even if the neglect patient perceived a stimulus as complete, he might not necessarily express the perception of the stimulus correctly in the drawing. A different approach has been advocated by some researchers (for a discussion see Weiskrantz, 1990). Instead of asking the patients what they 'see', perception in the blind hemifield can be studied

behaviourally. For example, Pöppel et al. (1973, p.295) were the first to apply this technique. The blindsight patients were asked to move the eyes to the position where they "guessed" the light had been presented.

Third, a further factor to produce a false completion effect might be the familiarity of the stimulus. If the figure is familiar and its form highly predictable, the patients might resort to the use of the generic term of the object as closest approximation to what they saw. Warrington (1965) reported a higher number of completion with figures that could be readily named and argued that they were completed more often than other stimuli due to their familiarity. Fourth, Bender and Teuber (1946) found that only objectively complete figures were perceived as complete by the hemianopic subjects and attributed the observation to residual vision in the affected visual field. Sergent (1988) discovered completion in only two subjects out of which one had residual vision in his impaired visual field. Some of Gassel and Williams' subjects (1963) had retained some visual function in the hemianopic field but, as the authors put it, "this by no means constituted the entire phenomenon" (Gassel & Williams, 1963, p. 232). However, to avoid confusion of the issues, patients with residual vision should be excluded from completion studies. Similarly, patients with macular sparing should not be included. A fifth caveat regarding false positive completion responses concerns the control of eye movements. Non-neglect hemianopic patients tend to direct their visual axis towards the hemianopic field to compensate for their visual field defect. Therefore, completion can be caused by perception of the object in the intact fields (see Gassel & Williams, 1963). Short presentation times up to 150 ms have been used to avoid deviation from the central fixation. However, short presentation times might be too short for the patient to perceive anything at all or to complete a stimulus. Torjussen (1978) solved the dilemma of eye fixation control and desirable long exposure times by presenting the stimulus figures as prolonged, high intensity flash-induced afterimages, thus achieving complete control of eye movements and allowing long inspection times simultaneously. Recently Marcel (1998) used the same technique as Torjussen (1978) and reported that even after a 15 minute gap of firing the flash gun, the evoked afterimage could be perceived and had not changed. This observation is relevant as potential interference of retinal stabilisation effects can be excluded. Retinal stabilisation describes the phenomenon

of image fading when the image is stabilised on the retina (Ditchburn & Ginsborg, 1952). A characteristic of retinal stabilisation is that fading and fragmentation of the pictorial stimuli tend to follow gestalt principles (Pritchard, 1961).

To conclude, completion is not an all-or-none phenomenon. Some patients with hemianopia do not display any completion at all, and those who report completion do not perceive complete figures in every trial. According to Pollack et al. (1957), 43% of their hemianopic patients displayed completion which is comparable to Warrington's (1962) figure of 55%. This result is discordant with Poppelreuter's (1917) and Gassel and William's (1963) view that hemianopics use completion as a normal mechanisms to compensate for the visual field loss. If this theory held true, every hemianopic subject would complete.

Fuchs' (1921) interpretation of completion in terms of Gestalt principles which was based on his observation that only symmetrical stimuli elicit completion has to be modified, too. Warrington (1960, 1965) who explicitly addressed this issue, unlike most of the above studies, has shown that complex figures can be subject to a completion process although she reported an increased tendency of completion for symmetrical figures in the later study (Warrington, 1965). The tentative hypothesis that symmetrical figures are more likely to be perceived as complete can be carefully supported by analysing the interaction between completion and unilateral versus bilateral presentation of the figure since only when two halves of a circle are presented to the visual fields the figure can be called truly and objectively symmetrical. The data show a stronger tendency of the patients to complete objectively complete figures where each half is projected to each visual field. Poppelreuter (1917), Fuchs (1921) and Pollack et al. (1957) reported completion of objectively incomplete stimuli. However, in Pollack et al.'s study (1957) most of these patients were confused and the authors conceded that the experimental paradigm had influenced the patients in favour of a completion response. On the other hand, Bender and Teuber (1946), Warrington (1962), Torjussen (1978), Sergent (1988) and Marcel (1998) collected evidence for an enhanced effect on completion through objectively complete stimuli.

Torjussen (1978) interpreted his results as interhemispheric interactive processes that are facilitated by mirror-symmetrical stimuli. Three stimulus patterns were used: A whole-, a half- and a half-displaced circle. The results showed completion with bilaterally symmetrical figures but not with objectively incomplete ones. Torjussen (1978) ruled out residual vision. He rather suggested "that under certain stimulus conditions visual function may be elicited in the hemianopic fields", i.e. visual processing in cortically blind areas (Torjussen, 1978, p.19). In Torjussen's (1978) study, patients did not report any stimuli when the projection was confined to the hemianopic field. The author proposed "an interaction between the stimulated areas on both sides of the vertical midline (and hence an interhemispheric interaction) that alters the function in the hemianopic side. The results further suggest that the effect of this interhemispheric interaction is facilitatory. It facilitates the detection of the stimulus portion falling in the hemianopic field, otherwise neglected when presented alone" (Torjussen, 1978, p.19). It also seemed crucial to position the stimuli mirror-symmetrically across the midline between the intact and impaired visual fields which enhanced the facilitatory interaction effect. Torjussen (1978) furthermore proposed that these effects were mediated through midbrain structures. Marcel (1998) applied the same technique as Torjussen (1978) and extended the stimulus set for two hemianopic patients. Torjussen's observations (1978) received confirmation. Only objectively complete stimuli were completed. If stimuli are symmetrical across the hemifields, they are seen completely. However, if symmetrical stimuli do not fall symmetrically with regard to retinal eccentricity, the pattern in the blind field is usually not seen.

We have now established some evidence that symmetrical (Poppelreuter, 1917; Fuchs, 1921; Torjussen, 1978; Marcel, 1998) and objectively complete stimuli (Bender & Teuber, 1946; Warrington, 1962; Torjussen, 1978; Sergent, 1988; Weiskrantz, 1990; Marcel, 1998) elicit a completion response more readily in commissurotomised and hemianopic patients. Furthermore, the data of the completion literature suggest an association of completion with hemianopia plus neglect (Pollack et al., 1957; Warrington, 1962; Sergent, 1988). A completion response to linguistic material has been demonstrated in a study by Kinsbourne and

Warrington (1962). Six patients with left hemianopia were examined. Letter sequences that could represent the end of a word were briefly presented to the intact visual field. The tendency to complete geometrical figures was correlated with the tendency to respond with a complete word.

In the next section, we will present an experiment that will investigate the question whether processing of mirror-symmetrical linguistic material is facilitated in neglect patients. An involvement of completion in the bisection of short (Halligan & Marshall, 1988) and long lines (Ishiai et al., 1989) has been postulated. Chatterjee (1995) drew parallels between the processing of linguistic stimuli and lines in neglect patients by showing that a power function describing the bisection of lines can also be applied to the error patterns of single word reading.

4.3. Processing of palindromes in neglect dyslexia

4.3.1. Introduction

In a recent single case study, Shillcock et al. (1998) showed that the tested neglect patient found it less difficult to read symmetrical (palindromic) words compared to non-symmetrical (non-palindromic) words. Our study will further explore this symmetry effect.

Before presenting the data of the experiment, we will propose potential neural mechanisms of completion and symmetry effects. Torjussen (1978) and Sergent (1988) suggested interhemispheric facilitation as the underlying mechanism of completion. An alternative neuroanatomical explanation for completion could be provided by the receptive field distribution of the parietal cortex: The majority of neurons in area 7a of the parietal cortex has bilateral receptive fields with a small but significant number of them possessing receptive field centres in the ipsilateral visual field (Andersen et al., 1990). These neurons might receive information from the ipsilateral visual field via subcortical connections (Trevarthen & Sperry, 1973). A third possibility to explain completion is that a stimulus is completed by the intact hemisphere only on the basis of what is projected to the intact hemisphere. In other words, there is no interhemispheric interaction or ipsilateral projection. However, this explanation appears less likely as most of the studies presented above reported

completion mainly after presentation of objectively complete stimuli (Bender & Teuber, 1946; Warrington, 1962; Torjussen, 1978; Sergent, 1988; Weiskrantz, 1990; Marcel, 1998).

Torjussen (1978) and Sergent (1988) further suggested that completion due to interhemispheric facilitation may be mediated by subcortical structures. Evidence for subcortical transmission has been provided in a number of split brain studies (Trevarthen & Sperry, 1973; Holtzman, 1984; Myers & Sperry, 1985; Sergent, 1986, 1987). However, the information that crosses hemispheres via subcortical channels "does not appear to include the name or identity of stimuli but rather is more contextual or associative in nature" (Myers & Sperry, 1985, p.249). Support from Torjussen's (1978) and Sergent's (1988) conjucture came from an unpublished study by Perenin and his colleagues (quoted by Weiskrantz, 1990). Two blindsight patients were tested for completion. Completion responses were clearly demonstrated in both patients, mainly for objectively complete stimuli. Particularly important in this context is the fact that one of the blindsight patients was hemispherectomised. Weiskrantz (1990, p.258) concluded: "The mediation" of completion "must be either by midbrain pathways or by ipsilateral inputs to the intact hemisphere, or both".

Since symmetry of stimuli appears to enhance the completion phenomenon (Poppelreuter, 1917; Fuchs, 1921; Torjussen, 1978; Marcel, 1998), we hypothesise that the symmetry effect is solely mediated by subcortical structures. The organic world is overwhelmingly composed of objects with at least some axis of symmetry. Therefore, one might expect that evolutionary older parts of the brain are geared to mediate symmetry information.

We have postulated that due to slowing down of the damaged hemisphere, interhemispheric communication is impaired. For this reason, symmetry effects mediated by interhemispheric facilitation (Torjussen, 1978) are not anticipated within the framework of our model However, the degree of desynchronisation is expected to be more marked between cortico-cortical fibers than between subcortical structures which are not as far apart in anatomical terms. Therefore, the observed symmetry effect for palindromic words (Shillcock et al., 1998) is anticipated by our analysis.

Sergent (1987) examined two commissurotomised patients in a lexical decision task. A four-letter high frequency word or a four-letter non-pronouncable non-word was presented in the centre of the visual field so that the first two letters fell in the left visual field and the last two letters in the right visual field. In this way, it was made impossible for the subjects to infer that a word or a non-word had been presented from the two letters appearing in one visual field. Sergent (1987) reported 70% and 75% correct word/non-word responses in each patient respectively. Also different subcortically mediated responses for words and non-words were revealed. For example, the patients produced a response like 'BEAST' or 'FEAST' after the presentation of the target word 'TEST' whereas no response was reported after the presentation of non-words. In other words, although the patients did not recover the meaning of the presented word, they recognised its familiarity.

In this study, we have performed two experiments: The first one uses the same stimulus material as Shillcock et al. (1998). We will attempt to replicate the symmetry effects obtained by Shillcock et al. (1998) for palindromic words. Based on Sergent's findings (1987), we hypothesise that familiarity enhances subcortical interaction and outweighs the effects of desynchronisation. In the second experiment, we will present palindromic and non-palindromic non-words to the patients. In this case, the hypothesis is that no symmetry effects should emerged when non-words, i.e. non-familiar stimuli, are presented to the neglect patients.

4.3.2. Experiment 1

4.3.2.1. Methodology

2.3.2.1.1. Inclusion/exclusion criteria and the neuropsychological assessment of subjects

The inclusion and exclusion criteria for neglect remain the same as it has been outlined in previous chapters. Furthermore all cerebral lesions sites were included in the study. Neglect patients with and without visual field defect took part.

4.3.2.1.2. Subjects

Patients from the stroke rehabilitation unit from Drumchapel Hospital, Glasgow, participated in our study. Five neglect stroke patients were examined[10]. The patients had suffered acute right hemisphere injury as demonstrated by CT- or MRI-scan without any record of previous cerebral injury. (see tables1 and 2 for patients' profile).

Table 1: Profile of patients subjects in study

Patient/age/ handedness/sex	**CT/MRI-lesion**	**Time from cerebral injury at time of testing; Experiment 1/2**
Neglect Patients		
1/82/R/F	R deep temporal infarct	4/5 weeks
2/79/R/F	R fronto-parietal infarct	8 weeks
3/74/R/F	R parietal infarct	8 weeks
4/73/R/F	R fronto-temporo-parietal infarct	10 weeks
5/74/R/M	R basal ganglia	10/10 weeks
	R fronto-occipito-parietal infarct	

Table 2: Patients' performance in star cancellation task, visual acuity scores and presence of visual field loss.

	Star cancellation tests		**Left visual field loss**	**Visual acuity**
	1	**2**		
	Side, number of stars cancelled			
Neglect Pts.				
1	R/18	R/23	-	N.8
	L/0	L/14		
2	R/17	-	-	N.12
	L/0			
3	R/26	-	+	N.12
	L/12			
4	R/15	-	+	N.12
	L/0			
5	R/25	-	+	N.12
	L/10			

Note. Only patient no. 1 performed two star cancellation tests. Her first set of scores indicate the performance immediately before the first experiment. The second test was performed on the day of the second experiment. The + sign indicates the presence, the - sign the absence of a visual field loss.

[10] Formal ethical approval had been obtained by the West Ethics Committee, Glasgow.

4.3.2.1.3. Apparatus

Materials were presented on an Apple MacIntosh LC 475 computer black and white monitor. The programme for the experiment was written on PsyScope 1.1.

4.3.2.1.4. Design

The dependent variable was the number of correctly read stimuli. The independent variable was symmetry of the words with two levels (symmetrical, non-symmetrical).

4.3.2.1.5. Material and procedure

Methodology and stimuli were adopted from Shillcock et al. (1998). Thirtysix palindromes were paired with 36 control words of the same length and approximate word frequency (CELEX lemma frequency; frequency out of 17.9 million words), number and summed frequency of neighbours about the first letter of the word, number and summed frequency of body neighbours of one, two and three letters. The palindrome and non-palindrome pairs also shared the initial two letters and were between three and nine letters long (appendix 6a).

The stimuli were presented in 18 pt bold courier font centred on the computer screen (see appendix 8d for the instructions to the subjects). Presentation of each word was preceded by a centrally located cross which appeared on the screen for 200 ms. The cross was followed by the stimulus with unlimited inspection time for the patient. Once the patient was satisfied with his/her response, a new trial was started by the experimenter pressing a button. Unlimited inspection time was chosen because of the severity of neglect. The subject read each word aloud and responses were transcribed by one examiner and recorded for further analysis. A practice session of ten items preceded the experiment proper.

4.3.2.1.6. Results

A binomial test was performed to analyse the responses to the palindromic material compared with the control stimuli. Subjects no. 3 and 5 did not commit any dyslexic

errors at all and are therefore not included in the analysis. The analysis revealed that subject no. 1 correctly identified significantly more palindromes than control words (z = -1.63, p = 0.05). No symmetry effects were discovered in patient no. 2 and 4 ($z = 0, p > 0.05$; $z = -1, p > 0.05$, respectively).

To summarise, we have succeeded in demonstrating a significant symmetry effect in one out of the five neglect patients. The results have replicated the findings reported in the single case study of Shillcock et al. (1998). In the next experiment we will test the hypothesis that no symmetry effect should emerge in palindromic non-words. Non-palindromic non-words were used as control material.

4.3.3. Experiment 2

4.3.3.1. Methodology

4.3.3.1.1. Inclusion/exclusion criteria and the neuropsychological assessment of subjects

The inclusion and exclusion criteria were the same as in experiment 1.

4.3.3.1.2. Subjects

Only subjects no. 1 and 4 participated in the second experiment (tables 1 and 2). The reason why not all five patients were followed up for the second experiment was of clinical nature. One patient was not willing to participate in the second experiment.

4.3.3.1.3. Apparatus

Materials were presented on an Apple MacIntosh LC 475 computer black and white monitor. The programme for the experiment was written on PsyScope 1.1.

4.3.3.1.4. Design

The dependent variable was the number of correctly read stimuli. The independent variable was symmetry of the non-words with two levels (symmetrical, non-symmetrical).

4.3.3.1.5. Materials and procedure

Twenty eight palindromic pronouncable non-words were paired with 28 non-palindromic pronouncable non-words (appendix 6b). The palindromic and non-palindromic non-words shared the same consonant-vowel configuration and number of letters in the stimulus (three to eight letters). The stimuli were printed in symmetrical capital letters (I, O, A, U, M, T, V, W) to create symmetrical stimuli at the word level.

The procedure of presentation was identical to experiment 1. A practice session of ten items preceded the experiment proper.

4.3.3.1.6. Results

A binomial test did not reveal any symmetry effects for the non-words, neither in patient no. 1 ($z = 0.37$, $p > 0.05$) who had read palindromic words significantly better than non-palindromic words nor in patient no. 4 ($z = -1.13$, $p > 0.05$) who had not displayed a symmetry effect in the previous experiment.

4.3.4. Discussion of experiments 1 and 2

We tested a group of neglect patients in a series of experiments which investigated the processing of symmetrical words and non-words. Our hypotheses were confirmed by the results: We found symmetry effects for palindromic words. One out of five neglect patients made fewer errors when reading symmetrical words compared with reading non-symmetrical words. In contrast, no such effect emerged when the neglect patients were presented with palindromic and non-palindromic non-words.

In the review of the completion literature, we have found evidence that neglect is associated with completion (Pollack et al., 1957; Warrington, 1962; Sergent, 1988). Furthermore, completion is reported more often in association with symmetrical material that is objectively complete (Torjussen, 1978; Sergent, 1988; Weiskrantz, 1990; Marcel, 1998).

Based on these observations, we have interpreted symmetry effects for palindromic words in a neglect patient (Shillcock et al., 1998) as completion behaviour: The part of the symmetrical stimulus that is projected to the intact hemisphere 'facilitates' completion, i.e. the perception of the neglected corresponding part of the symmetrical stimulus through interhemispheric activation (see Torjussen, 1978; Sergent, 1988). We have also argued, extending Torjussen's (1978) and Sergent's (1988) analysis that in neglect patients both completion *and symmetry* effects are mediated through the evolutionarily old subcortical parts of the brain. From this it follows that interhemispheric desynchronisation effects subsequent to cerebral damage are less pronounced between corresponding subcortical structures compared to cerebral areas that are connected through cortico-cortical association fibres. The distance between two anatomical structures has implications for desynchronisation. The greater the distance, the more marked the degree of desynchronisation. Consequently, the observed 'subcortical' symmetry effect is predicted by our temporal diplopia theory.

In contrast, it was proposed that symmetrical non-words are not subject to completion behaviour. This hypothesis was based on Sergent's observation (1987) that words and non-words are processed differently in split brain patients. We have attributed the differential processing of words and non-words in Sergent's study (1987) to the fact that the former are familiar stimuli, the latter are not. More specifically, a word possesses a mental representation which is accessed after integrating the information of the two hemispheres, a non-word has no corresponding mental representation.

We argue that familiarity of a symmetrical stimulus initiates the interaction of the two hemispheres. In patients who display symmetry effects, this interaction outweighs the effects of desynchronisation. Shillcock et al. (1998) described an interesting behavioural pattern in their patient in terms of the time course of his responses. When given unlimited inspection time of the stimuli, the patient showed significant improvement during the course of inspecting individual stimuli, reporting significantly fewer errors in his final guesses compared with his initial response. The

patient's exchange of information between the two sides of the brain appears to be slowed down and integration of information leading to a correct response was eventually achieved but only at considerable latencies (5 s to 2 min). In our study, we have extended the paradigm by presenting symmetrical and non-symmetrical words and non-words to neglect patients. Concordant with Sergent's results (1987) we found different response patterns to symmetrical words and non-words. A symmetry effect was observed for words but not for non-words. We speculated that the reason for a failure to find a symmetry effect in the second experiment is the fact that non-words, being unfamiliar to both hemispheres, did not precipitate interhemispheric interaction. Therefore, the effects of desynchronisation were not overcome.

However, there is a caveat. An alternative interpretation has to be addressed why non-words did not elicit a symmetry effect. The second experiment involving patient no. 1 who had displayed the symmetry effect in the first experiment was conducted two weeks after the first session. A star cancellation test was performed on each occasion. The scores of the second star cancellation test (table 2) clearly show that patient no. 1 had made a considerable recovery. Neuro-imagining studies have demonstrated that the recovery from neglect is associated with improved metabolic and perfusion rates of the cortical areas in the damaged hemisphere (Vallar, 1993). Therefore, during the course of patient no. 1's recovery, it is conceivable that the ipsilesional cortex reasserted its control over subcortical processing. For this reason, a potential symmetry effect for symmetrical non-words might have disappeared as the subcortical processes were overshadowed by superior cortical processing.

4.3.5. Conclusion

Although the symmetry effect for words does not appear to be a general phenomenon in the neglect population, it nevertheless provides evidence that Shillcock et al.'s patient (1998) was not a unique case. It seems that the symmetry effect characterises lexical processing in some neglect patients and that it can ameliorate performance in neglect dyslexia. The study adds further evidence to the importance of figural

goodness in visual perception. Symmetry effects for words were interpreted as interhemispheric completion on a subcortical level.

We also demonstrated that a symmetry effect did not emerge for non-words. It was suggested that differential processing of non-words on a subcortical level were the underlying mechanism for the absence of the symmetry effect.

Chapter Nine

Phantom limbs and supernumerary limbs in unilateral neglect

1. Introduction

In this chapter, we will present a single case study of a neglect patient who reported a supernumerary arm that was attached to her chest. Cases of supernumerary limbs or related delusional ideas are rare in the literature (Ehrenwald, 1930; Pineas, 1932; Van Bogaert, 1934; Gilliat & Pratt, 1952; Critchley, 1953; Weinstein et al., 1954; Fredericks, 1963; Halligan et al., 1993; Halligan & Marshall, 1995b; Halligan et al., 1995; Worthington & Beevers, 1996; Mazzoni et al., 1997; Vuilleumier et al., 1997). The investigation was concerned with the general 'binding' problem of body schemata. Furthermore, we addressed the relationship between perception and the body image. The study also explored the issue of rational, non-random preference responses in unilateral neglect (Marshall & Halligan, 1988).

In the first part of this chapter, we will present an introduction to the phenomenon of phantom limbs which will be followed by a discussion of the evidence on supernumerary limbs after cerebral injury and unilateral neglect.

2. Phantom limbs: Incidence and symptoms

After amputation of an arm or a leg, 95 to100% of patients experience the sensation of phantom limbs, i.e. the illusory perception of a non-existent limb (Bors,1951; Henderson & Smyth, 1948). Phantoms of other body parts can occur as well, like phantom penis, phantom bladder, rectum, breast (Melzack, 1990), phantom larynx and eye (Critchley, 1950).

Patients have reported a striking reality of the experienced sensation. Initially, patients describe the phantom as having a defined shape that is similar to the somato-sensory sensation of the normal limb before amputation. The phantom limb is

experienced to move in space normally and to integrate with the rest of the moving body. With time, the size and shape of the phantom limb may change. The leg or arm can fade so that the leg and hand might float unattached in the air. Alternatively, the limb might gradually telescope into the stump so that only the hand or the foot remains attached to the stump (Melzack, 1990).

However, the absence of a body part is not a requirement for the perception of a phantom limb. A known side effect of a brachial plexus avulsion is the occurrence of an imaginary "third" arm without any damage to the paralysed arm itself. Conomy (1973) investigated a group of 18 patients with spinal injuries for disturbances of their body image. The most common form of body image disorder was the changed perception of the body in space with 15 out of 18 patients experiencing this anomaly. The patients perceived their limbs as being in a different position than in their visually perceived location. Legs were more often affected than the upper extremity. Often the patients reported that their legs were floating upwards from the bed extended at knees or ankles and flexed at the hips. The second-commonest perceptual abnormality was the disorder of posture and movement. One patient exclaimed that his legs were "bent up underneath (his) body" and that his toes were forced into unnatural positions "like they are all turned down into the bottom of my foot" (Conomy, 1973, p.846). The least frequent disorder of body image were misinterpretations of size and continuity of limbs. Patients hallucinated increase of body parts in size. Only one subject reported a gap in his body image where a segment of body was felt as missing between parts that could be felt. Also subjects who have received spinal anaesthesia (e.g. Miles, 1956; Prevoznik & Eckenhoff, 1964) or a peripheral anaesthetic block of the sensory and motor nerves of an arm report the presence of a phantom limb in 94% of cases – a figure comparable to 95 to 100% in amputees and paraplegics (Melzack & Bromage, 1973). Melzack and Bromage reported (1973) similar perceptual properties in the experimentally induced phantom limbs compared to post-amputation phantom limbs.

3. Theories of phantom limbs

The classical clinical explanation of phantom limbs maintained that the sensation is caused by dissected axons and the formation of "neuromas" and scar tissue in the

stump. This view is now regarded as obsolete. Studies have demonstrated that the injection of local anaesthetic and surgical removal of the altered stump tissue is usually unsuccessful (Ramachandran, 1993).

Conomy (1973) summarised several theories that seek to explain the sensation of phantom limbs after spinal chord injury. One theory claimed that the area of trauma in the spinal chord acts as a false synapse to transmit postural information. An analogy was drawn to causalgic pain after crushing injuries of peripheral nerves. A different approach hypothesised the autonomic nervous system as an alternate route for postural and kinetic information from the lower bodies to the central nervous system. A third theory postulated distortions of the body image due to activity in the distal part of the intact spinal chord. Finally, it was proposed that even in seemingly complete dissections of the spinal chord the preservation of a small number of intact axons cannot be excluded. These few surviving neural pathways might be the source of triggering the changes of the perceived body image.

The definition of the body image was expressed by Head and Holmes (1911/1912, p.189) in the following way: Past impressions "may rise into consciousness as images, but more often, as in the case of spatial impressions, remain outside central consciousness. Here they form organised models of ourselves which may be termed 'schemata'. Such schemata modify the impressions produced by incoming sensory impulses in such a way that the final sensations of position, or of locality, rise into consciousness charged with a relation to something that has happened before".

Although Critchley (1950b, p.335) acknowledged that the continuous input of visual, tactile and proprioceptive information is important to form a body image, he stressed that "a body image of a sort exists in the absence of any one of the foregoing factors. Thus, the blind have their own kind of body image". According to Critchley (1950b, p.335), the perception of a phantom limb "shows how resistant the body image is to the effects of mutilation. So firmly rooted is it that it may even require a cortical ablation (or an intercurrent hemiparesis) to cause it to disappear".

Melzack (1990) took the argument further by postulating a "neuromatrix" as the underlying neuroanatomical correlate of the body image. Melzack (1990) defined neuromatrix as a Hebbian-type neuronal population that is genetically laid down.

Parallel and cyclical processing of sensory input with diverging and converging loops of neuronal activity eventually create a distinct "neurosignature", a distinct pattern of activity within the neuromatrix and whose configuration is influenced by sensory input. According to Melzack (1990), further support for this theory is provided by studies that demonstrated phantom limb phenomena in children with congenital aplasia. The traditional view on this issue maintained that phantom limb sensations do not occur if the limb is lost before the sixth or seventh year of age (e.g. Critchley, 1950). A different argument in favour of the neuromatrix is the fact that phantom limb sensations and pain re-emerge after therapeutical spinal chord dissection including a bilateral sympathetic block and even ablation of the somato-sensory cortex. However, Pollock et al. (1957) described a case where the phantom pain in the foot stump was alleviated by spinal anaesthesia. Furthermore, the discovery of so-called 'mirror neurons' seems to provide some evidence for a neuroanantomical substrate of the neuromatrix. Mirror neurons are a class of nerve cells that are found in the pre-motor cortex. Animal studies have shown that these neurons discharge when the monkey observes hand actions performed by another individual but only if the hand movements are similar to the action coded by the neuron (Rizzolatti & Fadiga, 1998; Rizzolatti et al., 1999). Rizzollatti and Fadiga (1998, p.81) proposed "that the internal motor copies of the observed actions represent the neural basis for understanding the meaning of actions made by others". It has also been suggested that imitative behaviours in young infants like tongue protrusion (Heiman et al., 1989) are mediated by mirror neurons (Rizzolatti et al., 1999). In short, Melzack's concept of the neuromatrix (1990) implied that the representations of the body image are strongly integrated in wide-spread areas of the brain and that these representations continue to exist even if peripheral sensory input is interrupted – either temporarily as in local anaesthesia techniques or permanently after amputation or spinal chord dissection.

A more specific theory but compatible with Melzack's neuromatrix (1990) was put forward by Ramachandran (1993) in the form of his "remapping hypothesis". In Ramachandran's study (1993), a patient suffering from so-called 'referred sensation' was investigated. In this case the arm had been amputated. The term 'referred

sensation' describes the phenomenon that tactile stimulation of certain areas of the face are experienced as emerging both from the face and the amputated limb. Ramachandran (1993) interpreted this observation as support for the view that sensory information originating from the face is "invading" the somato-sensory area in the Penfield homunculus that was formerly allocated to the arm. The underlying mechanism for this "invasion" could be either sprouting of new synaptic connections or unmasking of already existing pathways. The changes due to long term neuroanatomical reorganisation can be demonstrated several weeks after altering the input pattern of sensory information. Merzenich et al. (1984) amputated the middle finger of adult primates. Within two months the cortical area which originally had received input from the middle finger started to respond to stimulation of the adjacent fingers. Calford and Tweedale (1990) demonstrated short-term changes, probably due to unmasking, which developed within minutes. The digital nerve supplying the middle finger of a flying fox was anaesthetised. Within 20 minutes it was found that the cortical area corresponding to the middle finger could now be stimulated by adjacent digits.

The scale of reorganisation of cortical maps is considerable. Although it was known that somato-sensory maps do change (e.g. Merzenich et al., 1984), the extent of change was dramatically underestimated. Reorganisation in the range of 1 to 3 mm had been documented. However, Pons et al. (1991) studied cortical reorganisation in macaques twelve years after upper limb amputation. It was found that the cortical area that had originally supplied the upper limb could be activated by stimulation of the lower face. Pons et al. (1991) therefore demonstrated reorganisation of at least 10 mm. Yang et al. (1994) reported changes in the somato-sensory map of up to 35 mm using a magneto-encephalographic technique (see also Ramachandran et al., 1992). Ramachandran (1993) argued that this dramatic remapping process might be the underlying mechanism for phantom limb sensation. According to this theory, the experience appears because tactile and proprioceptive input from neighbouring somatosensory areas is projected into the cortical area of the lost limb. "Consequently, spontaneous discharges from these tissues would be misinterpreted as arising from the missing limb and might therefore be felt as a 'phantom' " (Ramachandran, 1993, p.10419).

A different study (Flor et al., 1995) using neuro-magnetic imaging techniques documented a strong direct relationship between the amount of cortical reorganisation and the magnitude of phantom limb pain after arm amputation. However, no correlation was found between cortical change and non-painful phantom phenomena.

Spitzer (1996) proposed a different theory developed from a model of self-organising feature maps. According to this theory, cortical reorganisation processes sustain the sensation of a phantom limb over time but the crucial mechanism that causes the perception of the phantom limb is situated at the spinal level. Spitzer (1996) based his theory on the supposed clinical difference of a phantom sensation in amputees and paraplegics. It is claimed that paraplegics "do not develop phantom sensations or develop phantoms which are clinically different from the phantoms of amputees. Phantom sensations in paraplegic patients are weak, they lack detail, and occur months after the onset of paraplegia" (Spitzer, 1996, p.275). Spitzer (1996) then claimed that input noise from the deafferented primary sensory neurons in the spinal chord causes both the subjective experience of the lost limb immediately after amputation and long term cortical reorganisation. Since in paraplegics information transmission is interrupted at the spinal level, the input noise from the peripheral sensory system cannot be transmitted. Hence, the supposed absence or difference in phantom limb sensations. Unfortunately, Spitzer (1996) did not define the qualitative differences of the phantom sensation in amputees and paraplegics. It is obvious that in the former case a limb has been removed and in the latter not.

However, Melzack and Bromage (1973) claimed that 95 to 100% of paraplegics experience phantom sensations. In a later paper, Melzack (1990, p.89) stated that "total section of the spinal cord at thoracic levels leads to reports of a phantom body including genitalia and many other body parts in virtually all patients". Conomy (1973) examined 18 spinal chord patients with regard to changes of the body images and reported cases where patients experienced disordered perception of limbs in space within minutes of the trauma. Similarly, Spitzer's claims (1996) are not concordant with the findings that "the presence of a phantom arm that resembles the descriptions of phantom limbs by amputees and paraplegics" could be induced by a brachial plexus block (Melzack & Bromage, 1973, p.261). Also, Spitzer's theory

(1996) cannot account for the existence of phantom limbs after a spinal anaesthetic block (e.g. Miles, 1956). In all three cases, paraplegia, brachial and spinal block, no input noise should be transmitted to the cortex. However, phantom limbs are experienced under these conditions. Finally, Bors (1951) examined a group of 50 patients with segmental lesions to the spinal chord. 100% of these patients experienced phantom limbs. Furthermore, another group in this study consisted of seven paraplegics that had also lost a non-paralysed limb. Bors (1951) reported that the intensity of the paraplegia phantom was much stronger when only the third, fourth and fifth finger had been lost. On the other hand, when the forearm had been amputated the amputation phantom was more intense than the paraplegia phantom. Taking all these arguments together, Spitzer (1996) will have to take a different approach to the problem of phantom limbs.

Weinstein et al. (1954) stressed the distinction between patients who suffer from *delusional* reduplication of parts of the body and patients who experience the *illusion* of a non-existing limb. Subjects who suffer from phantom limbs as discussed above fall into the latter category. In the next section, we will discuss the phenomenon of a supernumerary phantom limb after cerebral damage, where the distinction between these two classes is not as clear.

4. The supernumerary phantom limb after cerebral injury

Cutting (1978) examined 100 patients after acute left- or right-sided hemiplegia. An abnormal attitude towards an acute hemiplegia was found to be a common symptom independent of the side of cerebral damage. Anosognosia and anosognosic symptoms were reported in 87% of right hemisphere patients and in 54% or left hemisphere patients. These so-called negative symptoms (Halligan et al., 1995) included anosodiaphoria (lack of appropriate concern towards the hemiplegic side), feelings of non-belonging or misoplegia (hatred of the limb). Some patients display positive symptoms like supernumerary phantom limb, kinaesthetic hallucinations, delusional reduplication and somatoparaphrenia. The delusional ideas associated with these symptoms can include abnormal bodily experiences like duplication, feelings of alienation and detachment of body parts (Halligan et al., 1995). The distinction

between supernumerary phantom limb and somatoparaphrenia is not clear-cut. The term somatoparaphrenia was first used by Gerstmann (1942; quoted by Halligan et al., 1995) and referred to "cases of delusional elaboration in which the affected limbs were involved in peculiar illusory or confabulatory ideas" (Halligan et al., 1995, p.173). These positive symptoms after cerebral damage are rare. Cutting (1978) did not find a single case of supernumerary phantom limb in his study.

One of the earliest and most detailed accounts of somatoparaphrenia is a study by Ehrenwald (1930; quoted by Halligan et al., 1995) whose patient complained of a "nest of hands" in his bed. Since then only few clinical studies have been concerned with the phenomenon of extra limbs (Gilliat & Pratt, 1952; Critchley, 1953; Weinstein et al., 1954; Fredericks, 1963; Halligan et al., 1993; Halligan & Marshall, 1995b; Halligan et al., 1995; Worthington & Beevers, 1996; Mazzoni et al., 1997; Vuilleumier et al., 1997).

Before embarking on a discussion of the underlying mechanisms, we will compare the details of the patients' history and symptoms from some of the more recent cases in the literature (table 1). The patient K.R. studied during our project will be included. A more detailed presentation of our patient will be provided at a later point.

Table 1: Summary of patient details (adapted from Worthington & Beevers, 1996, modified and extended).

	K.R.	Worthinton & Beevers (1996)	Halligan & Marshall (1995b)	Mazzoni et al. (1997)
Age (years)	73	72	80	66
Sex	female	female	male	male
Time since trauma (months)	2-3	2-3	6	within 1
Nature of trauma	cerebro-vascular accident (CVA)	CVA	CVA	CVA
Lesion site	almost entire right middle cerebral artery	right middle cerebral artery	right middle cerebral artery	right nucleocapsular region, right corona radiata
Visual fields	left homonymous hemianopia	left homonymous hemianopia	left homonymous hemianopia	intact
Visual neglect	present	present	present	absent
General anosognosia	fluctuating	absent	absent	absent

General delusional ideas	fluctuating	absent	absent	absent
Extent of phantom	left hand and arm	left hand only	left hand only	entire left arm
Location	centre of chest, sometimes "roaming about"	left side	right upper leg	left shoulder
Perceived Origin	onset of stroke, associated with reported amputation	onset of stroke	?	8 days after stroke
Physical attachement to patient's body	sometimes attached to body	never attached to body	sometimes attached to body	sometimes attached to body
Appearance	"heavy"	slightly larger than other hands	"concrete"	almost normal but shorter
Persistence	intermittently present	intermittently present, always in existence	?always present	only present when eyes closed
Function	useless	useless	useless	obeys to commands
Dressing	not covered by clothes	went in left sleeve	-	-
Sensation	can sometimes feel it	can sometimes feel it	can feel it	can feel but not see it
Affect	initially distressed, later used to it	bemused but compliant with questioning	puzzled, distressed	puzzled and distressed

	Halligan et al. (1993)	Weinstein et al. (1954) - Case 1	Weinstein et al. (1954) - Case 2	Weinstein et al. (1954) - Case 3
Age (years)	65	57	24	51
Sex	male	female	male	male
Time since trauma (months)	2-3	within 1	within 1	4
Nature of trauma	CVA	probably metastatic carcinomatosis	closed head injury	closed head injury
Lesion site	right basal ganglia	right cerebral oedema, mid-brain and pons	? left hemiparesis	? right hemiparesis
Visual fields	left homonymous hemianopia	left homonymous hemianopia	intact	intact
Visual neglect	present	probably present	?, tactile extinction	absent
General anosognosia	absent	present	present	present
General delusional ideas	absent	last week before death	present	present

Extent of phantom	left hand and arm	left hand and part of arm	two pairs of legs	two eyes (his left eye had previously been removed), two heads, two bodies, four arms, four legs but one person
Location better	top left corner of torso	lying across the abdomen,	hips	?, patient "can see with left eyes"
Perceived Origin	associated with reported amputation	onset of stroke	onset of trauma	onset of trauma
Physical attachment	sometimes detached from body	sometimes detached from body	sometimes attached to body	sometimes attached to body
Appearance	sometimes similar to other limbs, sometimes feels "dead"	"bigger, hot, heavy"	?	similar to other limbs
Persistence	intermittently present	intermittently present	intermittently present	intermittently present
Function	sometimes obeys commands but	useless	useless	less functional
Dressing	not covered by clothes	?	?	?
Sensation	could occasionally see and feel it	could feel and see it	could sometimes feel them	could sometimes feel them
Affect	puzzled by it, distressed when questioned	occasionally called it "ridiculous", cheered up when talking about it	?	?

	Vuilleumier et al. 1997
Age (years)	64
Sex	female
Time since trauma (days)	2
Nature of trauma	operative removal of meningioma
Lesion site	pre-dominantly right parietal lobe with involvement of left parietal lobe
Visual fields	?

Visual neglect	present
General anosognosia	absent
General delusional ideas	absent
Extent of phantom	four lower limbs
Location	below pelvis
Perceived Origin	onset of trauma
Physical attachment	always attached to body
Appearance	normal, equal in size,
Persistence	always present
Function	"there are 2 legs on each side, maybe to help each other"
Dressing	?
Sensation	heavy
Affect	distressed

A number of questions regarding the aetiology and classification arise immediately after this overview that will be addressed in the following sections:

a) Are supernumerary phantom limb sensations and phantom limb sensations after spinal chord dissection or after amputation related phenomena?

b) Should cases of supernumerary limb perception be classified differently if the patient is suffering from various sets of delusional ideas?

c) Do neglect and anosognosia exacerbate the symptoms of supernumerary phantom limbs?

d) Is the site of cerebral injury of any significance?

4.1. Theories of phantom limb sensation and the supernumerary phantom limb

The theories of phantom limb sensation after spinal chord injury presented above are irrelevant in this context because they are based on pathological processes associated with the injured spinal pathways. However, all conditions that can cause the

perception of a phantom limb have one thing in common namely the loss of afferent information either temporarily as in brachial plexus block or spinal anaesthesia or permanently as after limb amputation, brachial plexus avulsion or spinal chord dissection. Similarly, in all supernumerary limb patients from table 1, a sensory loss in the affected side of the body has been documented - maybe except for Weinstein et al.'s subjects (1954) in which the clinical symptoms were not entirely clear. Case 1 from Weinstein et al.'s study (1954) was reported to suffer from impaired perception of proprioception and vibration whereas the tactile sense to single stimuli appeared intact. Case 2 and 3 only suffered from an impaired perception of simultaneous stimulation. No other sensory impairment was mentioned in these two cases. It follows that both Melzack's neuromatrix hypothesis (1990) and Ramachandran's remapping theory (1993) are applicable to the supernumerary limb patients.

To conclude, we hypothesise that the 'conventional' phantom limb sensation and the perception of supernumerary phantom limb after cerebral trauma are related phenomena. However, the question about the nature of the impairment in subjects 2 and 3 of Weinstein et al. (1954) remains.

4.2. The supernumerary limb and other delusional ideas

Weinstein et al. (1954, p.53) expressed no doubt about the classification of his cases: "...delusional reduplication cannot be regarded either as (1) a specific defect resulting from the destruction of any particular area of the brain[11], (2) the manifestation of a perceptual disturbance caused by the interruption of a particular afferent system, or (3) a manifestation of an alteration in the 'body scheme' ..." . Apart from experiencing extra limbs, Weinstein et al.'s patients (1954) also suffered from a whole set of delusions.

Less clear is the case described by Mazzoni et al. (1997) whose general neuropsychological assessment was within normal range apart from mild neglect. The authors hypothesised that sensation of the supernumerary limb could not have been caused by any generalised or partial cognitive decline. Mazzoni and colleagues

[11] In a recent review chapter, Weinstein (1996) stressed the particular role of the right hemisphere for reduplicative phenomena. More specifically, environmental and reduplication of body parts are more frequently associated with lesions of the right hemisphere, whereas phenomena involving person, object, temporal and self-reduplication are less lateralised.

(1997) proposed the patient's subcortical lesion which then alters the sensory input to the higher somato-sensory cortical areas involved in body image as the crucial mechanism in eliciting the illusory perception of the extra limb. Like in Mazzoni et al.'s study (1997), Worthington and Beevers' (1996) subject performed within average range on verbal intellectual tasks, had insight into the consequences of her stroke and showed no other reduplicative phenomena.

However, quite rightly it is pointed out that despite a relatively unimpaired performance in cognitive function, psychological factors in creating the perception of an extra limb cannot be excluded (Worthington & Beevers, 1996). Halligan et al.'s (1993) case study is particularly interesting in this context. Their patient displayed a completely rational approach to all topics apart from his delusional belief that he possessed a second left arm. The patient was also fully aware of the irrationality of his claim regarding the extra limb, but nevertheless adhered to it. Halligan et al. (1993) excluded psychodynamic factors in the origin of the third limb as there was no psychological benefit for the patient who clearly got distressed when interrogated about this issue. The authors proposed an alternative explanation according to which the supernumerary phantom limb is a derived phenomenon from the contradictions within a fluctuating belief system. The dilemma of "1. I have a normal right arm, 2. I have a paralysed left arm and 3. I have a normal left arm" might lead to the disturbing conclusion of "I have three arms" although the patient acknowledged his hemiplegia most of the time (Halligan et al., 1993, p.165). Indeed, these mechanisms of the unconscious can never be excluded in the perception of a supernumerary phantom limb, neither in patients who appear to be insightful and lucid let alone in patients whose awareness and cognitive functions are impaired. As for the original question whether patients with different sets of delusional ideas should be classified differently from patients plagued 'only' by the delusional belief of an extra limb the answer is yes - but mainly for the reason that one is even less likely to find a purely neuroanatomical mechanism for the origin of the supernumerary phantom limb in patients with multiple delusional beliefs. Furthermore, mechanisms shared between the two patient groups can never be excluded.

4.3. The role of neglect and anosognosia in the supernumerary phantom limb

Out of the eight patients from table 1, four displayed clinical symptoms of neglect, one was likely to have suffered from neglect and three subjects did not show signs of neglect. With respect to anosognosia, four patients had no awareness of the consequences of their illness and four did have insight. We will not embark on a discussion whether and how anosognosia and neglect could be related.

Neglect might conceivably exacerbate the two proposed pathological mechanisms of the supernumerary phantom limb, namely both the impairment of transmission of sensory afferent information and, as Halligan et al. (1993), suggested the conflict of the subconscious between two realities concerning the paralysed limb ("my arm is paralysed" versus "my arm is not paralysed"). As for the former process, proprioceptive and tactile information could still be generated and relayed but the integration at the necessary level might be impaired. This failure of peripheral feed-back might lead to the illusory perception of an extra limb like for example after a peripheral nerve block.

With respect to the latter mechanism, the subconscious conflicts between the two realities could be reinforced by fluctuations of both neglect symptoms and anosognosia. To neglect or to be unaware of a paralysed arm could mean for the patient that everything is in order and working. Short-lived recovery from neglect and anosognosia will then clash disturbingly with the previous assumption that everything is as it should be.

4.4. The site of cerebral damage and the supernumerary phantom limb

Seven of the nine patients in table 1 had suffered damage to the right hemisphere. The one patient with left hemisphere damage was not particularly typical since he had sustained a severe head injury. Halligan et al. (1993) quoted two studies that documented the sensation of a supernumerary phantom limb after left hemisphere damage (Pineas, 1932; Van Bogaert, 1934). Furthermore, Vuilleumier et al. (1997) reported a single case study of a patient who complained of four legs after the surgical removal of a para-sagittal meningioma. The operation caused damage to both parietal lobes. However, the right hemisphere had suffered more destruction

than the left. Whether this prevalence of right hemisphere trauma is a real trend remains to be seen. It is difficult enough to extract this potentially disturbing piece of information from a right hemisphere patient. Aphasic left hemisphere patients are even less likely to be identified as sufferers from supernumerary phantom limbs.
In a recent review of the reduplication literature, Weinstein (1996) concluded that the reduplication phenomenon of body parts is mainly associated with right hemisphere damage. What's more, Moser et al. (1998, p.174) claimed that reduplicative phenomena are "secondary to temporal-limbic-frontal dysfunction giving rise to a distorted sense of familiarity and impaired ability to resolve the delusion via reasoning".
A possible explanation for the low incidence of supernumerary phantom limb has been put forward by Mazzoni et al. (1997). It is proposed that subcortical lesions with preserved cortical structures are an essential condition for the supernumerary phantom limb and that it is for this reason that cases are so rare. However, this hypothesis has not received support by the clinical history of our patient K.R. who had suffered a massive right middle cerebral artery infarct which involved both subcortical and cortical areas.

In summary, we hypothesise that the perception of a phantom limb and the experience of a supernumerary limb in unilateral neglect are related disorders. To corroborate this claim patients who report a supernumerary limb but also suffer from a multitude of delusional ideas should be excluded from the relevant studies. Furthermore, it appears that unilateral neglect and anosognosia exacerbate the underlying mechanisms that produce the perception of an extra limb. As for the lesion site, right hemisphere damage seems to be associated with the supernumerary limb experience more frequently than left hemisphere damage.

5. Supernumerary arms and body schemata in unilateral neglect

5.1. Introduction

Ramachandran and Rogers-Ramachandran (1996) reported two cases of right hemisphere strokes causing unilateral neglect accompanied by left-sided hemiplegia and anosognosia which involved denial not only of the subject's own paralysis but

also that of a similar patient (or a collaborator). They concluded that at least some anosognosic patients will refuse to acknowledge a paralysis in another patient, and suggested that access to the subject's own body schemata may be necessary for making judgements about another person's.

In general, such a relationship between perception and non-sensory representations has a long history in psychology, as in "analysis-by-synthesis" (Neisser, 1967) and, for instance, currently informs some approaches to lexical representation (Pulvermüller, 1998). As examples of the latter, the comprehension of the word red is taken to involve activity in the parts of the visual system responsible for colour perception, whereas the comprehension of the verb to dig might involve activation in the centres associated with skilled, voluntary action. In the current investigation, we are concerned with the relationship between perception and body schemata in the special case of non-conscious perception in the neglected hemifield, as it might be influenced by the subject's experience of a supernumerary limb.

5.2. Methodology

5.2.1. Inclusion/exclusion criteria and the neuropsychological assessment of subjects

The criteria to classify the patient as a neglect patient are the same as for all studies described in the thesis. The patient had no record of a past neurological and psychiatric history.

5.2.2. Subject

The patient was a 73 year old retired secretary with a past medical history of paroxysmal atrial fibrillation and myocardial infarction. She was two months post-onset of the cerebral trauma at the time of testing. The CT-scan showed infarction of almost the entire right middle cerebral artery area. Clinically she was severely impaired by the cerebro-vascular accident and suffered dramatic fluctuations of her level of consciousness. Neurological examination revealed a dense left-sided hemiparesis, left sensory loss and a left visual field loss that was difficult to establish due to her neglect. K.R. exhibited classical features of neglect. Most of the time she sat slumped in her chair with her gaze directed towards the

right. In the star cancellation task she only cancelled eleven out of 27 small stars on the right hand side of the page. When asked whether she had finished the star cancellation test, she replied "no, I have not done the stars over there, yet" whilst making a gesture with her right hand towards the left side of the page. Despite a certain awareness of space to her left, she did not succeeded in crossing more stars than she had already cancelled. The patient's insight into her illness varied drastically, almost from minute to minute. One moment she would acknowledge her impairment and the next she would insist on going to the kitchen on her own to make a cup of tea.

We were alerted to the fact that K.R. experienced a supernumerary limb by her physiotherapist. During one physiotherapy session, K.R. expressed concern about the correct execution of her task because "Stumpy", her third arm, which was attached to the middle of her chest, got in the way. We subsequently interviewed her three times about her extra limb. We have included the unabridged interviews to give an accurate impression of the patient's perception of events.

Interviewer: "Jenny *(the physiotherapist)* told me about your arm. You call it Stumpy. Do you remember?

K.R.: *(Remains silent).*

I: How many arms have you got?

K.R: One, two, three, four.

I: Four. Where are they?

K.R.: Here is one with the arm *(points to the middle of her chest).*

I: And where are the other arms?

K.R: I don't know where the other arms are.

I: Where is your third arm? Can you see it?

K.R: It is usually sitting here *(points to the middle of her chest again).*

I: Is it one or two?

K.R.: Just the one.

I: Does it do things you want it to do?

K.R.: No, no, no.

I: What does it do?

K.R.: It just sits there. When I discovered it first it was roaming about. I kept thinking of The Monkey's Paw.

I: But now you are not so scared any more?

K.R.: No.

I: Is it there all the time?

K.R.: Yes.

I: Can you see it just now?

K.R.: No.

I: Can you just feel it?

K.R.: I can't even feel it. It's a dead weight.

I: Does it help you dress yourself?

K.R.: No, I have to keep moving it.

I: What about the leg? Is there another leg.

K.R.: No, no, no".

The next interview was conducted five days later.

I: "How many arms have you got?

K.R.: Two.

I: You told me you had three.

K.R.: No, three hands.

I: Where are they?

K.R.: *(She has her left arm across her chest with the left hand resting on the right shoulder. She counts by pointing with the right hand).* One *(points to the left hand),* two *(she makes a gesture to include her right hand)* and three *(points to the left hand again).* That's 'Tinky Poo', that's what I call it *(points to her left hand again).*

I: Does your third hand move at all?

K.R.: First time I discovered it, it moved. Thought it was a monkey's paw.

I: Where was it at the time?

K.R.: There *(points to the left hand which is still resting on her right shoulder).*

I: Were you scared?

K.R.: Yes, but then I said it's only a hand. Then I looked up to see whether anybody had an amputation. Then I looked to see whether I had an amputation. Then I

shouted out where is my arm or something and caused consternation but the doctor explained to me afterwards that this is quite a natural thing.

I: Now you are used to it.

K.R.: I am used to it but find it a nuisance.

I: Why?

K.R.: Imagine you are getting washed and you are trying to find a place for this to put where it doesn't slip.

I: You mean your third hand?

K.R.: Yes".

Four months later, we conducted a follow-up interview with the patient in a nursing home which was now her permanent domicile. In the star cancellation task, she still showed neglect and we had to sit on her right side during the interview. She was alert and witty and orientated in time, place and person. Her memory regarding the circumstances of the stroke remained unclear and blurred.

I: "How are you generally?

K.R.: I am dissatisfied with the way I am progressing.

I: In what way? What about your left side?

K.R.: I can move my left leg. I can walk allright. I say I can walk allright but some of the nurses say no, I can't walk. I say I go to the thing by myself. In fact, some of them even said you have got **three**, not three, two legs paralysed and I said I don't think so.

I: What about dressing? Can you dress yourself?

K.R.: Yes, I can but I am not very good at this business of taking things off. I always get stuck with my head in the sleeve of my nighty.

I: Now, four months ago you told me you had three arms. Is that right?

K.R.: That's right.

I: You called the hand 'Tinky Poo' and 'Stumpy'.

K.R.: No, I call it 'Flump' now.

I: You call it 'Flump'? Is it still there?

K.R.: That's it *(points at her paralysed left hand).*

I: That's 'Flump'.

K.R.: Yes.

I: So, how many arms have you got now?

K.R.: I have got two arms. I have always had two arms.

I: How many hands have you got?

K.R.: Two hands.

I: Can you show them to me?

K.R.: One *(lifts her right hand and then points with her right hand to the left hand)* and two.

I: You told me you had three arms. Do you remember?

K.R.: Yes, I told the doctor that I had another. It was my hand that was here *(points to her left hand again)* and he said no but that a lot of people get this experience.

I: When did your third hand disappear?

K.R.: No, I don't know.

I: So, it just disappeared gradually?

K.R.: What? The feeling that it wasn't mine?

I: No, the feeling that you had a third hand.

K.R.: Well, I still feel as if I have adopted it *(her left hand)* because I am sorry for it because it wasn't its fault but it got into that state. It just was at the wrong place at the wrong time. Poor old 'Flump'.

I: So, that's only two hands left. 'Tinky Poo' has disappeared then?

K.R.: No, that's 'Flump'.

I: You told me that you had a third hand that was roaming about on your tummy. It was always 'Flump'?

K.R.: Yes, always 'Flump'. When I woke up in the morning this thing was here *(points to her left hand)* and I got quite a fright. When the doctor saw it he said you know it's yours, don't you? And I said no, I didn't know it was mine.

I: It felt as if it did not belong to you.

K.R.: Yes.

I: But now you feel your left arm belongs to you?

K.R.: Yes, 'Flump' is mine".

In summary, K.R. presented with classical left neglect, anosognosia, anosodiaphoria (lack of appropriate concern of the hemiplegic side) and somatoparaphrenia with a feeling of 'nonbelonging' of the paralysed limb and the delusional belief of a supernumerary arm.

Four months later, the patient still suffered from severe unilateral neglect, lacked insight into her physical limitations although she conceded that some tasks are difficult for her. The feelings of 'nonbelonging' of her left arm have subsided and she did not suffer from the delusion of an extra limb anymore. However, when asked about the third hand specifically she was evasive and confabulatory. Her mention of three legs which was corrected quickly might be more than just a slip of the tongue and could represent remnants of her altered body schema although she had never claimed to have three legs. K.R. maintained that her third arm has always been identical with her paralysed left arm which she now calls 'Flump' but failed to explain this paradoxical situation. To rationalise her altered perception she referred to the doctor who called experiences of this kind common.

Based on K.R.'s descriptions of her experience, the supernumerary limb could almost be described as an allochiria-like behaviour where her left paralysed arm gets projected into the centre of her body but also leaves a 'trace' so that the patients counts three arms. Allochiria was demonstrated by K.R. in the butterfly copying task (see figure 1).

A. ORIGINAL **B. COPY**

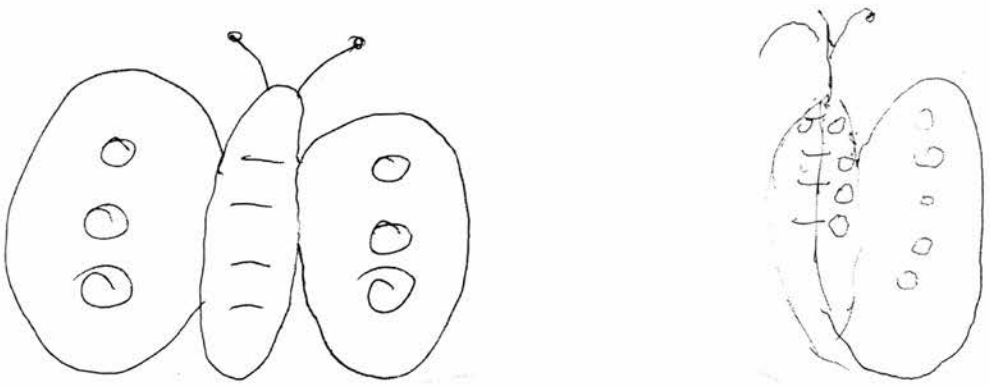

Fig. 1a: Butterfly to be copied, drawn by the experimenter.
1b: K.R.'s copy of the butterfly.

We devised a set of stimulus materials to investigate the relationship between perception and body schemata of the kind described by Ramachandran and Rogers-Ramachandran (1996). More specifically, to test the general hypothesis that non-conscious perception in the neglected hemifield was directly mediated by access to the subject's own body schemata.

5.2.3. Design

In this single case study, the dependent variable was the number of items chosen as the preferred version of the 'man in the suit' drawing (figure 2). The independent variable was the version of the drawing with two levels (supernumerary arm and normal version) which was nested in the perspective condition of the drawing with two levels (front and back view of 'the man in the suit' picture).

5.2.4. Material and procedure

The stimulus materials consisted of a pen and ink drawing of a man in a suit, which was photocopied to produce two versions of the original differing only on the left side of the drawing (see appendix 8e for the instructions to the patient). In the "normal" version the man was substantially symmetrical, in the "supernumerary" version the man had three different arms on the left, emanating from the shoulder. Individual A4 stimulus sheets were copied, in which the two versions appeared vertically aligned with the normal drawing in top or bottom position an equal number of times. A corresponding set of stimulus materials were also produced featuring the rear view of a similar individual, also with three arms on the left side of the drawing. The normal/supernumerary distinction was thus nested within a "front"/"back" condition (figure 2). Note that in the front supernumerary condition the right arm of the drawn man is non-normal, but in the back supernumerary condition it is the left arm of the drawn man that is non-normal. The stimulus sheets were presented to patient K.R. singly and centred on the mid-sagittal plane. The viewing distance was about 30 cm although body, head and eye movements were not constrained. The subject was asked to indicate which of the two versions she preferred.

If access to the subject's own body schemata mediates perception of the stimulus and, in particular, the difference between the normal and supernumerary versions, then we

might expect a difference between the back and front conditions, given that a different side of the individual is affected in each case. A significantly different preference between front and back conditions can only be explained with reference to the subject's own body schemata.

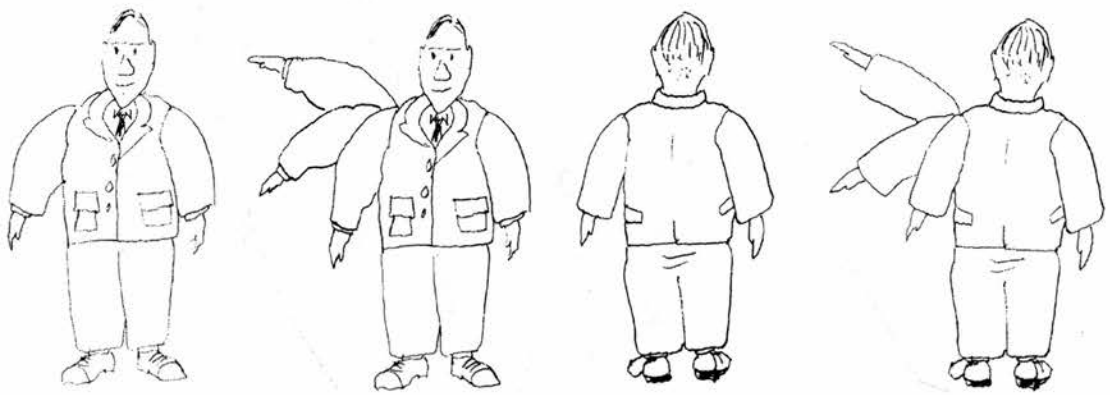

Fig. 2: Stimulus material: "The man in a suit" drawing. In the "symmetrical" and "supernumerary" version nested within a "front/back" condition.

5.2.5. Results

K.R. showed a significant preference for the supernumerary stimulus over the normal stimulus, as can be seen from the table 2. Pooling over all conditions, a binomial test gave $z = 2.17, p < 0.05$ (two-tailed).

Table 2: Preferences for normal and supernumerary stimuli, in front and back conditions.

	Normal	Supernumerary
Front	8	16
Back	8	16

The results are pooled over conditions in which the normal version appeared at the top and at the bottom of the sheet; exactly equal scores were recorded in each such

condition. As the table shows, an identical pattern obtained in the front and back conditions.

Throughout testing, K.R. consistently failed to report the genuine differences between the two versions of the drawing on each sheet, giving spurious differences on which she based her preference in each case, as below:

K.R. "I don't see anything. Maybe this one looks a bit funny. It looks as if there is a big plaster down his head.
K.R. He is the kinder face.
K.R. He is looking at me. He looks more relaxed".

When K.R.'s attention was finally drawn to the real difference within the pairs of pictures she was able to report the numbers of arms correctly.

5.2.6. Discussion

Our subject K.R. revealed a significant preference that was apparently based on visual material within the neglected hemifield. This result replicated the previous demonstration by Marshall and Halligan (1988) of non-conscious processing of neglected material in which the neglected material potentially contacts higher cognitive processing, causing a rational, non-random preference. In this paradigm, a subject with left-sided neglect due to right hemisphere damage was presented simultaneously with two line drawings of a house. In one of the two houses, the left side was on fire. Despite this significant difference, the two houses were judged as the same by the patient. However, in a forced choice task, she preferred the non-burning house significantly over the house on fire. Bisiach and Rusconi (1990) only partially replicated this effect. In their study, four left-sided neglect patients were tested with very similar material. One patient refused to collaborate, one displayed random selection between the two types of houses and only two chose consistently one version of the house. Unlike in Marshall and Halligan's study (1988), the preferred choice was for the burning house in the two patients which Bisiach and Rusconi (1990, p.646) concluded was made "with total disregard of the

relevant difference and on the basis of other, insignificant or 'confabulated' differences found in the non-neglected portions of the drawings".

Our patient K.R. produced a non-random preference but, as with Bisiach and Rusconi's subjects (1990), her choice was often accompanied with flowery confabulations ("well, he looks stocky. When he is walking it makes 'clonk, clonk'"). Unlike the past demonstrations of this effect, K.R.'s preference was related to her own physical state. K.R. demonstrated precisely the same preference in the front and back conditions. We can therefore only conclude that if the subject's own body schemata were involved in the perception, then it was in a way that was not sensitive to laterality. However, it has been shown that right hemisphere damage can impair aspects of conscious mental rotation and also that neglect might conceivably contribute to this deficit (Ratcliff, 1979). One might argue that the patient's identical performance in the front/back conditions might be due to impaired mental rotation rather than due to access to only abstract body schemata. In other words, the patient is aware of her body schemata but fails to perform correspondingly due to a constant left/ right confusion.

Ratcliff (1979) examined 59 men with left, right and bilateral cerebral injuries. The subjects were asked to make a left/right judgement under two experimental conditions. The stimulus material were schematic drawings of a man in either upright or inverted positions. In each trial only one hand was marked. The subjects were required to indicate which hand had been marked. The right posterior cerebral damage group made fewer mistakes in the upright but made significantly more in the inverted condition. In our experiment, we are assuming mental rotation has to occur to swing 'the man in the suit' around to see his front and vice versa. However, since the stimulus material was only presented in the upright condition, a claim of impaired mental rotation would be only a weak one although an exacerbating effect of neglect can not be excluded. Nevertheless, our interpretation of left/right confusion due to an impairment of mental rotation is supported by K.R.'s drawing of herself which she performed four months after the first experiment. In this drawing, the patient marked the *right* hand of the figure as 'Flump' which in reality is K. R.'s *left* paralysed arm (figure 3).

Fig. 3: Four months after the above experiment, the patient was asked to draw a picture of herself from a frontal perspective. She performed this task with a lot of skill. K.R. drew the picture on the very right edge of the piece of paper. On the left side of the drawing the right foot is missing. Interestingly, the person in the drawing has the head turned to the figure's right hand side. Furthermore, K.R. marks the right arm of the figure as 'Flump' which is K.R.'s left paralysed arm.

Furthermore, Vuilleumier et al. (1997) presented a single case study of a left neglect patient who developed an illusory reduplication of the lower limbs after the surgical removal of a menigioma. She claimed to possess four legs. In a Laterality Discrimination test which consisted of judging whether line drawings of body parts are from the body's left or right side, the patient displayed a severe deficit. The results were interpreted as a failure in right-left reversal and mental reorientation of relative positions in space. However, the patient had suffered bilateral parietal lobe damage with the right side being more affected.

Finally, it should be noted that in this general paradigm it is not feasible to exclude low spatial frequency information that could potentially be used to distinguish the two versions of the picture (Trevarthen & Sperry, 1973). Such processing is relevant to distinguishing one picture from the other but not to preferring one over the other. We claim that the phenomenon of supernumerary limbs and neglect can be explained within the same framework laid out by our theory. In the above sections we have

illustrated that neglect and the experience of supernumerary limbs could be associated. It has been argued in chapter 4, that intra- and interhemispheric desynchronisation of neuronal activity impairs the binding of information. Desynchronisation between the two hemispheres leads to incompatible information processing and neglect of the information processed in the damaged hemisphere is the consequence. Similarly, if there is loss of intrahemispheric synchronised activity combined with the imbalance between excitatory and inhibitory processes of a damaged cerebrum (Fieschi, 1980), the binding of information between neurons that are involved in the coding of the body image might be disrupted. The fragmentation of the body schemata together with the emergence of reduplicative phenomena ensues - be it in terms of Head and Holme's definition of body schemata (1911/12), in terms of Melzack's neuromatrix (1990), or due to desynchronisation between motor or pre-frontal mirror neuron populations (Rizzolatti & Fadiga, 1998; Rizzolatti et al., 1999). In some neglect cases, the product of the fragmented body schema is perceived in an allochiria-like manner on the non-neglected side (K.R. in our study; Halligan & Marshall, 1995b; Weinstein et al., 1954). In other cases the supernumerary limb's appearance is connected to the neglected side of the body (Halligan et al., 1993; Worthington & Beevers, 1996) which could be explained by the fluctuations of the hemodynamic and metabolic situation in the damaged hemisphere. Impairment of proprioceptive and sensory information processing from the neglected side of the body appears to be an additional necessary condition to cause the perception of an extra limb. We have seen that stimulation of the damaged hemisphere (Rubens, 1985; Pizzamiglio et al., 1990; Karnath et al., 1993; Vallar et al., 1995; see also cueing effects: Bisiach et al., 1981; Halligan et al., 1991; Brunn & Farah, 1991; Mattingley et al., 1994) can ameliorate neglect. Consequently, if there is no sensory feed-back from the neglected half of the body to the damaged hemisphere, the sequelae of desynchronisation are exacerbated.

Furthermore, right hemisphere damaged appears to be associated more frequently both with neglect and the experience of supernumerary limbs. We have hypothesised that the right hemisphere is more vulnerable to the effects of desynchronisation because the principle of coarse coding is more developed in the right hemisphere. The neuroanatomical substrate for coarse coding is large receptive fields. Coarse

coding has implications for synchronisation. The larger the receptive fields, the longer the distances cortico-cortical association fibers have to travel between levels. Therefore, if, as postulated, both neglect and the perception of a supernumerary limb are caused by desynchronisation, we would expect a higher incidence of neglect and supernumerary limb cases after right hemisphere damage. This hypothesis is borne out by the data (Brain, 1941; Critchley, 1950; McFie & Zangwill, 1960; Arrigoni & De Renzi, 1964; Benton, 1969; Faglioni et al., 1971; Gainotti & Tiacci, 1971; Gainotti et al., 1972; Chedru, 1976; Schenkenberg et al., 1980; Mesulam, 1981; Denes et al., 1982; Kinsbourne, 1987; Massironi et al., 1988; Heilman et al., 1993; Spiers et al., 1993; K.R. in our study; Halligan et al., 1993; Worthington & Beevers, 1996; Halligan & Marshall, 1995b; Weinstein, 1996)

5.2.7. Conclusion

In this case study, we have presented the rare case of a neglect patient who has experienced a supernumerary limb. The investigation is a novel extension of existing demonstrations of non-conscious processing in the neglected hemifield (Marshall & Halligan, 1988) to stimulus materials that reflect the physical and cognitive state of the subject. The materials are more versatile (in terms of showing front and back views, for instance) than the real patients or collaborators used in past studies. At the same time, there is no issue concerning the identification of the subject with the individual being viewed, as the stimulus object was a male cartoon character drawn on a piece of paper. Ramachandran and Rogers-Ramachandran (1996) speculated that it may be relevant for the subject to perceive the other also as fellow-patient. In at least some cases, comparable to K.R., perception of a pathological state in another may not be based on personal body schemata, or else the body schemata may be referred to at a level that has abstracted away from left/right differences. Furthermore, we have presented a unified account of neglect and supernumerary limbs within the framework of our theory.

Chapter Ten

Final summary and conclusions

The core of this thesis is a new model of unilateral neglect, the "temporal diplopia"[12] theory. Although the theory only captures qualitative aspects of neglect without making quantitative predictions as some models have (Halligan & Marshall, 1989; Mozer & Behrman, 1990; Smith, 1994; Chatterjee, 1995; Pouget and Sejnowski, 1995, 1996, 1999; Monaghan & Shillcock, 1998), it is nevertheless strictly constrained by neuroanatomical and electrophysiological evidence. In this summary, we will first present the main aspects of the theory in a nutshell. We will then discuss the empirical evidence obtained in the current study within the framework of our model before reaching the final conclusion.

1. The "temporal diplopia" theory

In chapter four, we have illustrated that cerebral damage after a cerebro-vascular accident dramatically changes blood perfusion (Olsen et al., 1981; Celisia et al., 1984), the metabolic milieu (Metter et al., 1986) and electrophysiological activity (Obeso et al., 1980; Jordan, 1993). Mainly the damaged hemisphere is affected by the changes but sometimes the contralesional side of the brain is found to be involved, too (Andrews, 1991; Buchkremer-Ratzmann et al., 1996).

In short, the data from imaging and elcetrophysiological studies provided evidence for slowing down of neuronal activity in the damaged hemisphere of stroke patients with and without neglect/extinction whereby the slowing appears to be more pronounced in the neglect group (Watson et al., 1977; Lhermitte et al., 1985; Spinelli et al., 1994; Viggiano et al., 1995; Doricchi et al.,1996; Pitzalis et al., 1997; Demeurisse et al., 1998). Further support for this analysis came from empirical studies (Bisiach et al., 1984; Birch et al., 1967; Rorden et al., 1997; Husain et al., 1997; Duncan, 1998).

[12] The term was originally used by Pöppel (1994) in connection with normal perception.

Synchronous activity is a widespread phenomenon in the central nervous system and has been proposed as a feasible model of neural encoding, binding and integration of information (Von der Malsburg, 1981; Singer, 1993, 1998; Singer & Gray, 1995). Furthermore, synchronisation has increasingly been implicated not only in low level sensory computations (Engel et al., 1991, 1991c; König et al., 1995; Roelfsema et al., 1996) but also in complex cognitive processing like memory, attention and consciousness (Crick & Koch,1990; Tononi et al., 1992; Eckhorn et al., 1992; Kinsbourne, 1993; Tiitinen et al., 1993; Pöppel, 1993; Pöppel & Schwender, 1994; Desmedt & Tomberg, 1995; König & Engel, 1995; Singer, 1995, 1998; Llinás et al., 1998).

We asked the question what would happen if synchronous activity were disrupted? If synchronicity mediates sensory and high level cognitive processing, the consequences of desynchronisation are expected to be grave. Confirmation for this hypothesis was provided by recent studies which analysed the temporal correlation of neuronal responses in amblyopic and strabismic animals. It was shown that impaired perceptual processing was associated with reduced synchronised neuronal discharge (König et al, 1993; Roelfsema, 1994). Fries et al. (1997) provided further evidence that disruption of synchronicity might lead to perceptual impairment as their study with cats in binocular rivalry conditions shows.

Slowing down of neuronal functioning in the damaged hemisphere of stroke patients has implications for synchronised activity. For synchronisation to be an effective encoding mechanism, neuronal discharge has to occur with a precision in the millisecond range (Von der Malsburg, 1981; Singer, 1993, 1998; Singer & Gray, 1995). Therefore, slowing down of activity will impair synchronous discharge. Furthermore, the longer the distance between two neuronal populations, the more synchronisation will decrease between these populations. Based on the above evidence, the "temporal diplopia" theory has made three claims:

Claim 1: Impaired synchronised neuronal activity *within* the damaged hemisphere and *between* the two hemispheres is the underlying neurophysiological mechanism of many symptoms observed in unilateral neglect patients.

Claim 2: The consequence of impaired intrahemispheric synchronisation is:

- Representations in the damaged hemisphere lose saliency due to a weakening of the electrophysiological signal. The binding and integration of information within the damaged hemisphere are impaired.

The consequence of impaired interhemispheric synchronisation is:

- The damaged hemisphere is out of phase with the undamaged hemisphere due to unilateral slowing down. The binding and integration of information between the hemispheres are impaired.
- The brain is faced with a processing dilemma of incompatible information: "Temporal double vision". The problem extends to both the sensory-motor system and cognitive processes.
  Conscious perception of some part of the contralesional world is not experienced. This unilateral loss of consciousness is mediated by a combination of active and passive mechanisms. There is active suppression of the damaged hemisphere by the intact hemisphere. Other examples of suppression of incompatible information are found in amblyopia, binocular rivalry and saccadic suppression. A passive mechanism for losing conscious representation of the neglected information is the diminished neuronal signals in the damaged hemisphere.

Claim 3: Unilateral neglect, therefore, does not exist as a neuropsychological entity. It is the product of a disrupted basic processing mechanism and the extreme manifestation on the spectrum of unspecific unilateral cerebral damage. Consequently, similar, but attenuated, patterns of impaired processing should emerge in stroke patients without neglect.

Five different experimental paradigms were used in our study to explore the above claims (chapters five to nine). The time bisection paradigm (chapter five), the rhythm

perception experiment (chapter six) and the inspection time paradigm (chapter seven) were designed to corroborate our hypothesis that processing in the damaged hemisphere is slowed down. A specific prediction was that slowing down is more pronounced in the neglect group compared to the non-neglect group.

2. Unilateral slowing down: The time bisection, rhythm perception and inspection time paradigm

The time bisection paradigm tested duration processing in stroke patients with and without neglect and in a group of normal control subjects (700 to 3300 ms) whereas the rhythm experiment investigated the perception of fast (500 to 700 ms) and slow rhythms (700 to 900 ms). Both experiments had been designed so that the task demands were exclusively sensory. The inclusion and exclusion criteria were strict. We selected only patients whose site of the lesion did not involve areas know to be involved in timing and rhythm processing. We also performed a set of memory tests to exclude patients with working and long term memory deficits. The data were analysed within the framework of scalar timing theory (Gibbon, 1977; 1981a,b; Gibbon & Church, 1984; Gibbon et al., 1984).

The obtained results fitted our hypotheses. The non-neglect group displayed consistent changes of *time* and *rhythm* perception predicted by unilateral slowing of the damaged hemisphere with none of the changes reaching significance levels. However, the data produced by the neglect group for the test intervals in the time bisection experiment were so inconsistent that the analysis did not yield any meaningful results. The deficit of duration perception in the neglect group was reflected by greater Weber Fractions with the difference approaching significance levels. The Weber Fraction represents the subject's ability to discriminate a specific stimulus. We attributed the neglect patients' failure to process the test intervals to impaired memory and attentional processes. The time bisection paradigm required the subjects to store both standard intervals in a memory buffer during the presentation of ten different consecutive test intervals. We concluded that the demands on attention and memory exceeded the capacities of the neglect group. To reduce the processing load, the rhythm perception experiment was designed. In this

paradigm, the test rhythm was played to the patient immediately after the presentation of the standard rhythm. Furthermore, the longest interval between two beats of the test rhythm was only 900 ms as opposed to the duration of 3300 ms in the time bisection experiment (see appendix 9 for a comparison of performance across experiments in patients who performed more than one experiment).

The different design of the rhythm experiment turned out to be successful: The neglect patients' data for the fast rhythms displayed consistent marginally significant response patterns. Also, the observed changes in rhythm perception of the neglect patients agreed with our hypotheses. However, the performance of the neglect group for the slow rhythms was again so erratic that the data could not be fitted into a regression analysis. These results suggest that neglect patients are able to process temporal information only within a very narrow time window centring around 500 ms; Griffiths et al. (1997) reported a single case study of a neglect patient who succeeded in processing a sequence of rhythmic stimuli presented over 650 ms but failed when the presentation time dropped to 260 ms.

Working memory function appears to be associated with the prefrontal cortex (Zatorre et al., 1994; D'Esposito et al., 1995, 1998; Knight et al., 1999). Sarnthein et al. (1998) extended working memory function to other cerebral areas. A model of working memory was proposed that involves the synchronisation between the pre-frontal and posterior association cortices by phase-locked, low-frequency brain activity. We have claimed that in stroke patients both intra- and interhemispheric processing is impaired. Our model can therefore account for some degree of working memory deficit in stroke patients with intact prefrontal cortices.

How can our analysis reject claims of interference from potential memory and attentional deficits? In fact, the observed changes of time and rhythm perception both in the non-neglect and neglect group could be attributed to attentional and working memory deficits rather than slowing down of the damaged hemisphere.

However, as for the non-neglect group this alternative interpretation of the data can be discarded as the non-neglect subjects had Weber Fractions that were of the same order (and even slightly better) as those of the control group. As far as the neglect

group is concerned, interference from memory deficits was minimised by performing memory tests as part of the selection process.

Nevertheless, we cannot exclude attentional deficits as the underlying mechanism for the altered fast rhythm perception. Controlling for attentional deficits in neglect patients is difficult, if not impossible, as one of the least disputed clinical symptoms of a neglect patient is his or her limited attention span. Therefore, the design of an experiment is of particular importance when working with neglect patients and should always take their processing limitations into account.

Furthermore, the increased Weber Fractions of the neglect group in both the time and rhythm perception experiments are consistent with the findings of Marshall and Halligan (1989). In their study, a left neglect patient displayed dramaticly increased Weber Fractions in the line bisection performance. Therefore, our results allow for the tentative hypothesis that an increase in the Weber Fraction is a basic pathology found in neglect patients.

Bearing the above restrictions in mind, we designed the inspection time experiment to test the time that is required to process information in the left, right or both visual fields correctly. We hypothesised that the processing load for the patients would be minimal as the experiment involved looking at the centre of a computer screen and reporting the components of trigrams. All patient groups coped well with the test situation. The following results that fitted our predictions were obtained: Overall the neglect group produced the smallest number of correct responses compared to the non-neglect group and the control group. The scores of the non-neglect group also suggested some processing deficit with the control group producing the highest number of correct responses. Unsurprisingly, the neglect patients required significantly longer inspection times for stimuli in the LVF than the non-neglect and control groups whereas performance in the RVF field was unexceptional compared to the other two groups. In contrast, the non-neglect stroke group did not perform significantly worse in the LVF when compared to the control group. However, a trend emerged, albeit tenuous, that indicates a processing deficit of the non-neglect group in the contralesional visual field. While the control group was significantly more accurate than the neglect population at inspection times as short as 120 ms in

the LVF, the non-neglect group required an inspection time of 200 ms to produce significantly more correct responses than the neglect patients. Before interpreting the above data as compatible with the predictions of our hypothesis, we again have to address the question of possible interference from attentional deficits. It has been argued that in the inspection time paradigm, the time for correct target processing was tested. Alternatively, one might say that not the processing time was measured but merely the time it takes to shift attention from the focus of attention to the target stimulus as the work of Làdavas and her colleague might suggest (Làdavas, 1990; Làdavas et al., 1990). In these studies, the authors claimed that both extinction patients and patients with neglect focus their attention on the right relative position. Therefore, the time to move attention across the right to a target in the LVF will necessarily produce longer inspection times. However, in the present study we have interpreted our results within the framework of a prior entry phenomenon. In a temporal order judgement task, Rorden et al. (1997) examined two patients suffering from extinction after unilateral right parietal damage. The patient was sitting in front of a computer screen on which first a central cross appeared. This cross remained in place for the duration of the trial to provide a continuous central fixation point. Then a short horizontal line appeared on the left side, the side of extinction, followed by a second short horizontal line. The task of the patient was to indicate on which side the line first appeared. The results showed that the line on the left had to precede the one on the right by 200 ms to be perceived as appearing first. Rorden and his colleagues interpreted their results as "a genuine delay in visual awareness itself" (Rorden et al., 1997, p.429). Within the framework of our theory, we attribute the increased inspection times to desynchronisation secondary to the slowed down processing of sensory information. In chapter four, we have illustrated that synchronised neuronal activity has been associated with consciousness and awareness (e.g. Singer, 1998). In so far, our view is in agreement with Rorden et al.'s interpretation of the data (1997). On the other hand, Làdavas' position remains untenable as long as no neurophysiological model of attention is put forward (Làdavas, 1990; Làdavas et al., 1990).

In summary, we interpret the results of the neglect and non-neglect patients in the time and rhythm perception experiments and the inspection time paradigm as compatible with the hypothesis that the processing speed of the damaged hemisphere is slowed down. A small caveat is that potential interference from attentional deficits in the neglect group can not be excluded from the analysis of the rhythm and time perception data.

In the remaining two experimental chapters (eight and nine), we have sought to unify and explain empirical neglect data within the framework of the "temporal diplopia" theory.

3. Synchronisation, symmetry and completion

In chapter eight, we reported the results of two experiments exploring stimulus properties in neglect dyslexia. The processing of symmetrical words and non-words straddling the left and right visual fields was investigated. In a recent single case study, Shillcock et al. (1998) showed that the tested neglect patient found it less difficult to read symmetrical (palindromic) words compared to non-symmetrical (non-palindromic) words. Our study has examined this symmetry effect further by adopting and extending Shillcock et al.'s methods (1998).

The "temporal diplopia" theory has claimed that the two hemispheres are desynchronised. Binding and exchange of information across the midline are impaired. Consequently, any symmetry effect is at first sight incompatible with our model (see also Spinelli et al., 1994; Viggiano et al., 1995). However, various authors have suggested that completion phenomena are associated with some behavioural responses of neglect patients. For example, an involvement of completion in the bisection of short (Halligan & Marshall, 1988) and long lines (Ishiai et al., 1989) has been postulated. Furthermore, Chatterjee (1995) drew parallels between the processing of linguistic stimuli and lines in neglect patients by showing that a power function describing the bisection of lines can also be applied to the error patterns of single word reading.

Consequently, we reviewed the existing completion literature and found evidence that neglect is associated with completion (Pollack et al., 1957; Warrington, 1962; Sergent, 1988). What is more, completion is reported more often in association with symmetrical material that is objectively complete (Torjussen, 1978; Sergent, 1988; Weiskrantz, 1990; Marcel, 1998). Torjussen (1978) and Sergent (1988) claimed that completion phenomena are mediated by subcortical structures. We extended Torjussen's (1978) and Sergent's (1988) analysis and hypothesised that in neglect patients both completion *and symmetry* effects are mediated through the evolutionarily old subcortical parts of the brain. From this it follows that interhemispheric desynchronisation effects subsequent to cerebral damage are less pronounced between corresponding subcortical structures compared to cerebral areas that are connected through cortico-cortical association fibres as distance between two anatomical structures has implications for desynchronisation. The greater the distance, the more marked the degree of desynchronisation. Consequently, the observed 'subcortical' symmetry effect is predicted by our temporal diplopia theory.

In contrast, it was claimed that symmetrical non-words are not subject to completion behaviour. This hypothesis was based on Sergent's observation (1987) that words and non-words are processed differently in split brain patients. We have attributed the differential processing of words and non-words in Sergent's study (1987) to the fact that the former are familiar stimuli, the latter are not. More specifically, a word possesses a mental representation which is accessed after integrating the information of the two hemispheres, a non-word has no corresponding mental representation. It is argued that familiarity of a symmetrical stimulus initiates the interaction of the two hemispheres. In neglect patients who show symmetry effects, this interaction outweighs the effects of desynchronisation.

In summary, the "temporal diplopia" theory can account for the observed symmetry effect and can make specific predictions regarding stimulus specificity in neglect behaviour. However, the predicted failure to elicit a symmetry effect with non-words could have an alternative explanation other than a familiarity effect. The second experiment (reading of non-words) involving the patient who had displayed the

symmetry effect in the first experiment (reading of words) was conducted two weeks after the first session. A star cancellation test was performed on each occasion. The scores of the second star cancellation test clearly showed that the patient had made a considerable recovery. Neuro-imagining studies have demonstrated that the recovery from neglect is associated with improved metabolic and perfusion rates of the cortical areas in the damaged hemisphere (Vallar, 1993). Therefore, during the course of the patient's recovery, it is conceivable that the ipsilesional cortex reasserted its control over subcortical processing. For this reason, a potential symmetry effect for symmetrical non-words might have disappeared as the subcortical processes were overshadowed by superior cortical processing.

4. Phantom limbs, supernumerary limbs and desynchronisation

The ninth chapter described a single case study of a neglect patient who reported a supernumerary arm that was attached to her chest. Our patient K.R. presented with classical left neglect, anosognosia, anosodiaphoria (lack of appropriate concern of the hemiplegic side) and somatoparaphrenia with a feeling of 'nonbelonging' of the paralysed limb and the delusional belief of a supernumerary arm. Four months after the initial examination, the patient still suffered from severe unilateral neglect, lacked insight into her physical limitations although she conceded that some tasks were difficult for her. The feelings of 'nonbelonging' of her left arm had subsided and she did not suffer from the delusion of an extra limb anymore. However, when asked about the third hand specifically she was evasive and confabulatory.

This chapter was concerned with the general 'binding' problem of body schemata and the disintegration of body schemata due to desynchronisation. Furthermore, we addressed the relationship between perception and the body image. The study also explored the issue of rational, non-random preference responses in unilateral neglect (Marshall & Halligan, 1988).

At first sight the perception of a phantom and a supernumerary limb appear to be related phenomena. We explored this intuition by reviewing and comparing the phantom limb literature with case studies of supernumerary limbs. We demonstrated

that theories of phantom limbs can indeed account for the emergence of supernumerary limbs. Therefore, it was hypothesised that the perception of a phantom limb and the experience of a supernumerary limb in unilateral neglect are related disorders. Furthermore, it appears that unilateral neglect and anosognosia exacerbate the underlying mechanisms that produce the perception of an extra limb. As for the lesion site, right hemisphere damage seems to be associated with the supernumerary limb experience more frequently than left hemisphere damage.

The experimental set up was motivated by a study of Ramachandran and Rogers-Ramachandran (1996). The authors reported two cases of right hemisphere strokes causing unilateral neglect accompanied by left-sided hemiplegia and anosognosia which involved denial not only of the subject's own paralysis but also that of a similar patient (or a collaborator). They concluded that at least some anosognosic patients will refuse to acknowledge a paralysis in another patient, and suggested that access to the subject's own body schemata may be necessary for making judgements about another person's. Therefore, the experiment of our study dealt with the relationship between perception and body schemata in the special case of non-conscious perception in the neglected hemifield, as it might be influenced by the subject's experience of a supernumerary limb.

The stimulus materials consisted of a pen and ink drawing of a man in a suit, which was photocopied to produce two versions of the original differing only on the left side of the drawing. In the "normal" version the man was substantially symmetrical, in the "supernumerary" version the man had three different arms on the left, emanating from the shoulder. Individual A4 stimulus sheets were copied, in which the two versions appeared vertically aligned with the normal drawing in top or bottom position an equal number of times. A corresponding set of stimulus materials were also produced featuring the rear view of a similar individual, also with three arms on the left side of the drawing. The patient was asked to chose the preferred version of the drawing that was placed in front of her.

Our subject K.R. revealed a significant preference that was apparently based on visual material within the neglected hemifield. This result replicated the previous demonstration by Marshall and Halligan (1988) of non-conscious processing of

neglected material in which the neglected material potentially contacts higher cognitive processing, causing a rational, non-random preference. We concluded that K.R.'s choice was related to her own physical state. However, K.R. demonstrated precisely the same preference in the front and back conditions. We can therefore only conclude that if the subject's own body schemata were involved in the perception, then it was in a way that was not sensitive to laterality. Alternatively, one might argue that the patient's ability to rotate the figure mentally was impaired (Ratcliff, 1979; Vuilleumier et al., 1997).

Furthermore, we claim that the phenomenon of supernumerary limbs and neglect can be explained within the same framework laid out by our theory. We have shown that neglect and the experience of supernumerary limbs can be associated. Our theory has hypothesised that intra- and interhemispheric desynchronisation of neuronal activity impairs the binding of information. Desynchronisation between the two hemispheres leads to incompatible information processing and neglect of the information processed in the damaged hemisphere is the consequence. Similarly, if there is loss of intrahemispheric synchronised activity combined with the imbalance between excitatory and inhibitory processes of a damaged brain (Fieschi, 1980), the binding of information between neurons that are involved in the coding of the body image might be disrupted. The fragmentation of the body schemata together with the emergence of reduplicative phenomena ensues - be it in terms of Head and Holme's definition of body schemata (1911/12), in terms of Melzack's neuromatrix (1990), or due to desynchronisation between motor or pre-frontal mirror neuron populations (Rizzolatti & Fadiga, 1998; Rizzolatti et al., 1999). In some neglect cases, the product of the fragmented body schema is perceived in an allochiria-like manner on the non-neglected side (K.R. in our study; Halligan & Marshall, 1995b; Weinstein et al., 1954). In other cases the supernumerary limb's appearance is connected to the neglected side of the body (Halligan et al., 1993; Worthington & Beevers, 1996) which could be explained by the fluctuations of the hemodynamic and metabolic situation in the damaged hemisphere. Impairment of proprioceptive and sensory information processing from the neglected side of the body appears to be an additional necessary condition to cause the perception of an extra limb. We have

seen that stimulation of the damaged hemisphere (Rubens, 1985; Pizzamiglio et al., 1990; Karnath et al., 1993; Vallar et al., 1995; see also cueing effects: Bisiach et al., 1981; Halligan et al., 1991; Brunn & Farah, 1991; Mattingley et al., 1994) can ameliorate neglect. Consequently, if there is no sensory feed-back from the neglected half of the body to the damaged hemisphere, the sequelae of desynchronisation are exacerbated.

Furthermore, right hemisphere damage appears to be associated more frequently both with neglect and the experience of supernumerary limbs. We have hypothesised that the right hemisphere is more vulnerable to the effects of desynchronisation because the principle of coarse coding is more developed in the right hemisphere. The neuroanatomical substrate for coarse coding is large receptive fields. Coarse coding has implications for synchronisation. The larger the receptive fields, the longer the distances that cortico-cortical associations fibers have to travel between levels. Therefore, if, as postulated, both neglect and the perception of a supernumerary limb are caused by desynchronisation, we would expect a higher incidence of neglect and supernumerary limb cases after right hemisphere damage. This hypothesis is borne out by the data (Brain, 1941; Critchley, 1950; McFie & Zangwill, 1960; Arrigoni & De Renzi, 1964; Benton, 1969; Faglioni et al., 1971; Gainotti & Tiacci, 1971; Gainotti et al., 1972; Chedru, 1976; Schenkenberg et al., 1980; Mesulam, 1981; Denes et al., 1982; Kinsbourne, 1987; Massironi et al., 1988; Heilman et al., 1993; Spiers et al., 1993; K.R. in our study; Halligan et al., 1993; Worthington & Beevers, 1996; Halligan & Marshall, 1995b; Weinstein, 1996)

5. Conclusion

Halligan and Marshall (1992) have called for the exploration of "principles" of malfunction in neglect patients. In this thesis, we have provided such a principle: Abnormal temporal integration and binding of information which impairs processing within the damaged hemisphere and between the two hemispheres. Our model is not the first to claim disruptions in the temporal domain. Abnormal temporal processing appears to be a fundamental problem as it has been associated with a number of neuropsychological and psychiatric disorders like dyslexia, dysphasia, autism and schizophrenia (Llinás, 1993; Merzenich et al., 1993; Tallal et al., 1993; Prather et al.,

1991, 1992, 1997). Why temporal malfunction leads to different clinical pictures in different patient groups is a question that warrants future exploration.

The empirical data collected in this thesis were interpreted as compatible with our "temporal diplopia" theory. In chapters five to seven, we provided data consistent with the claim that processing in the damaged hemisphere is slowed down. Chapters eight and nine illustrated the explanatory power of our theory by unifying existing empirical evidence of neglect.

As for the subject of future research, we would like to encourage studies that will explore different aspects of temporal processing, for example time production in stroke patients with and without neglect. However, the limitations of processing abilities in neglect should be borne in mind. We hope that our study has made a contribution that will facilitate future work in this field and help to shape an experimental design appropriate for exploring temporal processing in unilateral neglect patients.

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Appendix

1. Phonological Working Memory Test (Gathercole, 1995).

Perplisteronk
Loddernapish
Woogalamic
Blonterstaping
Skiticult
Tafflest
Frescovent
Bannow
Detratapillic
Contramponist
Brasterer
Empliforvent
Underbrantuand
Diller
Glistow
Pristoractional
Ballop
Penerriful
Reutterpation
Altupatory

2. Long term memory word repetition test from the CELEX data base (CELEX lemma frequency; frequency out of 17.9 million words).

	Frequency
Bed	244
Car	276
Boy	207
Book	269
Hand	440
Table	203
Woman	338
Water	432
School	389
Father	272

3. Stimuli of Inspection time paradigm (Hellige et al. 1989).

SEG	PES
DEG	KAG
GEF	KAF
FAS	FAP
PED	FES
FET	GES
GOP	KEF
GED	SEP
SOF	KED
TEF	FAK
DEK	SAF
FEP	POG
PEF	GAK
DEP	FEK
PAF	FEG
SEF	TEK
FOS	SEK
KES	KET

4. National Adult Reading Test, NART (Nelson, 1991).

CHORD	SUPERFLUOUS
ACHE	SIMILE
DEPOT	BANAL
AISLE	QUADRUPED
BOUQUET	CELLIST
PSALM	FAÇADE
CAPON	ZEALOT
DENY	DRACHM
NAUSEA	AEON
DEBT	PLACEBO
COURTEOUS	ABSTEMIOUS
RAREFY	DÉTENTE
EQUIVOCAL	IDYLL
NAÏVE	PUERPERAL
CATACOMB	AVER
GAOLED	GAUCHE
THYME	TOPIARY
HEIR	LEVIATHAN
RADIX	BEATIFY
ASSIGNATE	PRELATE
HIATUS	SIDEREAL
SUBTLE	DEMESNE
PROCREATE	SYNCOPE

GIST	LABILE
GOUGE	CAMPANILE

5. Visual acuity test (Hope et al., 1989).

N.5 renaissance

N.8 accession

N.12 examiner

N.18 passion

N.36 blood

The British Faculty of Ophthalmologists' test types.

- Test each eye separately
- Hold text at 30 cm from eye
- Record smallest type accurately read.

6. Palindromic versus non-palindromic stimuli.

a. Palindromic and non-palindromic words (Shillcock et al., 1998).

Palindromic:

3 letters:	bob, dad, dud, gag, mum, pap, pep, pip, pop, pup, tat, tit, tut, wow
4 letters:	noon, poop, sees, deed, toot
5 letters:	civic, kayak, laval, madam, minim, radar, rotor, sagas, sexes, solos, tenet
6 letters:	marram
7 letters:	deified, racecar
9 letters:	redivider, rotavator

Non-palindromic:

3 letters:	bop, dap, dug, gap, mud, pad, peg, pig, pod, pug, tap, tig, tug, woo

4 letters: norm, posh, sell, deck, toil

5 letters: cigar, kazoo, ladle, maple, mimic, rabbi, roost, sabre, seize, soapy, tepid

6 letters: malady

7 letters: raccoon, decibel

9 letters: roominess, reiterate

b. Palindromic and non-palindromic non-words.

Palindromic:

3 letters: MIM, TOT, VAV, VOV, VUV, VIV.

4 letters: MOOM, VOOV, WOOW

5 letters: AVOVA, WOMOW, TAVAT, MIVIM, OOMOO, VOTOV, OTITO, AMOMA, TIMIT, MUTUM

6 letters: TOMMOT, VADDAV, WOMMOW, MATTAM.

7 letters: ATTUTTA, TOOMOOT, VITOTIV

8 letters: MOOTTOOM, VOOTTOOV

9 letters: METUVUTEM, TATOVOTAT

Non-palindromic:

3 letters: FAS, GOF, FUB, FON, GOL, SIL

4 letters: HOAL, LOOF, NEAF

5 letters: TASER, GODER, CONIF, OALEY, MOFER, GENOR, SIRID, AMADY, ADINE, ODARY

6 letters: MISPER, GONNIG, PULLON, MONDIT.

7 letters: OSTERNY, BEADOON, POLETIN

8 letters: LOARGEEN, FOOSTOAM

9 letters: VARUSIVEN, GODIFERON

7. Patients' Histories:

Test	Patient Numbers	
Time Bisection Experiment	Neglect Patients:	No.1,2
	Non-Neglect Patients:	No. 8, 11
Rhythm Experiment	Neglect Patients:	No. 2, 3, 4
	Non-Neglect Patients:	No. 8, 9, 13
Inspection Time Experiment	Neglect Patients:	No.1, 3, 5
	Non-Neglect Patients:	No. 9, 10, 12
Palindrome Reading Experiment	Neglect Patients:	No. 2, 3, 4, 6, 7

Neglect Patients:

1. The subject was a right-handed, well educated 82 year old lady. She had graduated from university with a degree in French and German and had worked most of her life as a teacher, only interrupted for a few years to look after her two children. Recently, she had been on holiday in the USA visiting her son when she suddenly collapsed with a left hemiplegia and loss of consciousness. A CT-scan was performed and described a right mid-cerebral artery infarct. The site of lesion was not specified further. An angiography revealed the occlusion of the right internal carotid artery of 100% and of the left internal carotid artery of 50%. After three weeks the patient was transferred from USA to the stroke rehabilitation ward in Scotland. She had a past medical history of hypertension and mysthenia gravis. Her medication included ACE-inhibitors and beta-blockers. She was first seen for this study after a five months' stay on the ward. Her neglect symptoms were still described as severe by physiotherapists and nursing staff. The patient suffered from a dense hemiparesis on the left and showed no signs of visual field defects. She was sent home after six months on the stroke ward. Two months later, she was readmitted with partial seizures which were treated as post-stroke seizures. A new event was considered less likely. Support for this diagnosis came from a repeat CT-scan which showed a large well defined area of reduced attenuation in the right parietal region consistent with an old infarct. Her hearing was intact.

2. The patient was a right-handed 74 year old lady who had left school and worked all her life as an auxiliary in a nursing home. She was now widowed and lived on her own. She was admitted to the stroke unit with loss of consciousness and left hemiparesis. An MRI-scan showed a right parietal

infarct. She had smoked all her life and her past medical history was insignificant. Her medication only included Aspirin. Her neglect was described as severe by the staff. She suffered from a dense left hemiparesis and left homonymous hemianopia. Only a very slight hearing impairment could be established. Initially, she had no insight into her illness. She only gradually gained awareness of her illness.

3. The patient was a right-handed 79 year old lady. She had left school at 14 years of age, finished her training as a short hand typist. She finished her career in a demanding secretarial position. The patient was admitted with a left-sided hemiplegia. The CT-scan revealed a large ischaemic lesion in the right fronto-parietal area. She had a past medical history of mild hypertension and was a non-smoker. Her current medication was Aspirin. She was seen two weeks after admission. The patient suffered from a dense left-sided hemiplegia and had no signs of visual field defects. There was only a slight hearing impairment. Clinically, her neglect appeared severe. When asked by one of the physiotherapists how her left arm was she replied "this is not my arm. This is my friend's arm. She was a very affable lady with dramatic fluctuations of alertness and without any insight in her illness, at all.

4. Patient was a 82 year old right-handed lady who had left school at 14 and worked as a shop assistant for 6 years until she got married. She was admitted after collapsing at home. On examination she presented with a left-sided hemiplegia. No visual field loss and hearing impairment were established. The CT-scan documented an extensive area of infarction in the right deep temporal region. She was a non-smoker and her past medical history included atrial fibrillation and mild hypertension. Her current medication was Aspirin. She was first seen one week after admission. Her neglect was clinically not too severe. She managed to find her left arm by starting at the left should and tracing the way down. She was a pleasant, co-operative and increasingly alert lady with partial insight into her illness.

5. The patient was a 85 year old right-handed lady who was a retired theatre sister. She was admitted to the ward with a left-sided hemiplegia after collapsing at home. The CT-scan demonstrated a small area of low attenuation in the right frontal region extending into the right lateral ventricle to the cerebral surface. The lesion was consistent with an infarct. She had a past medical history of ischaemic heart disease. Her medication included nitrates, diuretics, anti-hypertensives and Aspirin. She was seen four weeks after admission. She suffered from moderate clinical neglect, a dense hemiparesis and did not display signs of visual field loss. She was a helpful, intelligent lady with hardly any insight into her problems.

6. The patient is a 73 year old retired secretary with a past medical history of paroxysmal atrial fibrillation and myocardial infarction. She was 2 months post-onset of the cerebral trauma at the time of testing. The CT-scan showed infarction of almost the entire right middle cerebral artery area. Clinically she

was severely impaired by the cerebro-vascular accident and suffered dramatic fluctuations of her level of consciousness. Neurological examination revealed a dense left-sided hemiparesis, left sensory loss and a left visual field loss that was difficult to establish due to her neglect. K.R. exhibited classical features of neglect. Most of the time she sat slumped in her chair with her gaze directed towards the right. When asked after her star cancellation test whether she had finished the star cancellation test, she replied "no, I have not done the stars over there, yet" whilst making a gesture with her right hand towards the left side of the page. Despite a certain awareness of space to her left, she did not succeeded in crossing more stars than she had already cancelled. In the second star cancellation task which was conducted four months later the patient crossed 17 stars on the right side of the page.
The patient's insight into her illness varied drastically, almost from minute to minute. One moment she would acknowledge her impairment and the next she would insist on going to the kitchen on her own to make a cup of tea.

7. The patient was a 74 year old gentleman who was a retired sales man. After complications following a triple bypass surgery he suffered multiple ischaemic infarction in the right basal ganglia, right occipital, parietal and frontal cortices as was confirmed by a CT-scan. He had a past medical history of myocardial infarction. On examination he presented with a left dense hemiplegia, a left-sided homonymous hemianopia and severe left-sided neglect. He was a helpful person with limited insight into his problems.

Non-neglect stroke patients:

8. The was a right-handed 72 year old gentleman who had left school at 14 years and from there had worked his way up to a business manager post. He was admitted to the ward with sudden onset of left-sided weakness and no loss of consciousness. The CT-scan showed a small ischaemic lesion in the parietal area. He suffered from a paralysis of his left arm and weakness in his left leg and had no visual field defects. No hearing impairment was established. His past medical history was unremarkable apart from slightly elevated cholesterol levels. He was a non-smoker. His medication included Aspirin. He was helpful, bright, had insight into his illness and was very verbose.

9. The patient was a right-handed 74 year old lady who had left school at 14 and then worked as a hair dresser and cleaning lady for most of her life. She was admitted with a left-sided hemiparesis. No visual field loss and hearing impairment were established.The CT-scan showed an area of fronto-temporal low attenuation on the right side which was consistent with an infarct. She had a past medical history of hypertension and polymyalgia rheumatica. Her medication included Aspirin and diuretics. She was a keen and motivated subject with insight.

10. The patient was a 88 year old right-handed lady. She had left school at 14 years worked as a shop assistant until she got married. She was admitted to

the stroke ward with a left-sided hemiparesis. The CT-scan revealed a large well-established infarct in the temporo-parietal area of the right hemisphere. Her past medical history included atrial fibrillation, hypertension and myocardial infarction. Her current medication was Aspirin. She was seen two weeks after admission and suffered from left hemiparesis. There was no evidence of visual field defects. She was an alert helpful lady and aware of the consequences of her stroke.

11. The patient was a right-handed 60 year old unemployed welder. He had been in this profession since he had left school at the age of 14 years. He was admitted to the stroke unit with left-sided weakness. Clinically no impairment of the subject's hearing could be established The CT-scan showed a well established subcortical infarct in the posterior limb of the right internal capsule. On auscultation a stenotic bruit over his right internal carotid artery was heard. He has been a long term smoker. Past medical history was not of any note. His only medication was Aspirin. He was seen six weeks after admission and suffered from a left paretic arm and left leg weakness. There was no visual field loss. His hearing did not appear to be impaired. He was an alert and helpful subject with insight into his situation.

12. The patient was a 60 year old right-handed gentleman who had left school at 14 years, first worked as a shop assistant and then as a salesman. He was admitted with a left hemiparesis after collapsing. The CT-scan documented a right-sided deep temporal infarct. There was a slight shift in the midline to the left. He was an ex-smoker with atrial fibriallation, mixed aortic and mitral valve disease, hypertension, non-insulin dependent diabetes mellitus and congestive cardiac failure in his past medical history. His medication included Digoxin, ACE-inhibitors, diuretics and anti-diabetic drugs. He was seen five weeks after admission and suffered from a left-sided hemiparesis with a slight improvement of his left leg. He had no visual field defects. He was a friendly patient with a realistic attitude towards his prospects in life.

13. Patient H was a 86 year old right-handed lady who was a trained nurse. She had worked all her life. She was admitted with a sudden onset of left-sided weakness. There was a slight impairment in her hearing. The CT-scan showed a small area of low attenuation in the subcortical area of the temporal lobe in the right hemisphere. In the past, she had suffered from insulin dependent diabetes mellitus and hypertension. Her medication included insulin, diuretics, anti-hypertensive and anti-diabetic drugs. She suffered from a paralytic left arm and left leg weakness. She was a helpful somewhat slow lady with partial insight into her illness.

8. Instructions to the subjects:

8a. The time bisection experiment

These instructions were read out to the subject while sitting on the right side of the subject. This technique was chosen to avoid possible misunderstandings caused by potential neglect dyslexia in the neglect population.

"During this experiment you will be wearing headphones. We will play you a set of two beeps to the left and the right ear.
The gap between the beeps may be short or long. When it is short, you will see the word "SHORT" on the screen. When it is long, you will see the word "LONG". The second beep is followed by the word "END" on the screen.
Then you will hear two beeps where the gap between them can vary in length. This is indicated by the word "TRIAL" on the screen.

Your task is to decide whether the length of the gap between the two beeps in the trial is closer to the short or the long gap which you have heard at the beginning.
If you think, it was closer to the short one say "short". If you think, it was closer to the long one, say "long".

Could you also repeat the word "go" as soon as you see the word "TRIAL". Stop saying the word "go" when you see the word "END" on the screen and give your response.

Thank you for your time".

As expected the subjects, in particular the neglect group, required more training sessions for this experiment than for the other ones. However, no subject ever complained that the task was too difficult. On the contrary, the non-neglect stroke group very much enjoyed participating in the experiments which were a change from the ward routine.
Interestingly, there did not seem to be any awareness at all in the neglect population about how erratic their performance was. Not once did the neglect patients express any concerns that the demands of the sessions were too great for them or had exhausted them.

8b. Rhythm experiment

These instructions were read out to the subject while sitting on the right side of the subject. This technique was chosen to avoid possible misunderstandings caused by potential neglect dyslexia in the neglect population.

"During this experiment you will be wearing headphones. We will play you beeps to the left and the right ear. These beeps form a steady rhythm. The rhythm can be fast or slow.

There will be two rhythms played to you. The first rhythm will be indicated by the number "1" on the screen, the second one by the number "2". The end of each rhythm is marked by the word "END".

Your task is to decide whether the second rhythm is the same as the first rhythm or different. If you think, it was the same, please say "same". If you think, it was different, please say "different".

Thank you for your time".

As above, no subject found the task too difficult. One neglect patient later revealed, after finishing the experiment, that she did not like wearing the headphones. Asked about the difficulty of the experiment, she did not find it too demanding.

8c. Inspection time experiment

These instructions were read out to the subject while sitting on the right side of the subject. This technique was chosen to avoid possible misunderstandings caused by potential neglect dyslexia in the neglect population.

"In this experiment a cross will appear in the middle of the screen for a short time. Please look at the cross.
The cross will then be followed by a funny sounding word which will also only appear for a short time. This word will be shown to you from top to bottom instead of from left to right as usual. It may appear on the left, the right or on both sides of the screen. The word will then be followed by a second object which covers the word up. Please say out loud what you saw and spell the letters out from the top to the bottom.

It is very important that you keep looking at the place where the cross was all the time, even when the word appears.

You can take your time in deciding what it was you saw. It is not important to be quick but to be accurate.

Thank you for your time".

No comments where made about the difficulty of the task. Every subject seemed to grasp immediately what they were requested to do.

8d. Reading task

These instructions were read out to the subject while sitting on the right side of the subject. This technique was chosen to avoid possible misunderstandings caused by potential neglect dyslexia in the neglect population.

"In this experiment a cross will appear in the middle of the screen for a short time. The cross will then be followed by a word. Please read out the word.

Thank you for your time."

The patients appeared to find it easy to comply with the experimental instructions. Those neglect patients who committed paralexic errors did not seem to be aware of them, i.e. did not show any signs of frustration.

8e. The supernumerary limb experiment

These instructions were read out to the subject while sitting on the right side of her. This technique was chosen to avoid possible misunderstandings caused by potential neglect dyslexia in the neglect population.

"Please look at the sheet of paper in front of you. You will see two drawings of a man in a suit, shown either from the front or the back. Please mark with your pen which drawing of the man you prefer.

Thank you for your time."

The patient found this task "very easy" but at the same time "pointless". She completed the experiment without any difficulties.

9. The performance of individual patients compared and contrasted across experiments:

• Patient number 1, a neglect patient, was tested in two different tasks: The inspection time and the time bisection experiment (tested at 15 and 41 weeks respectively). The star cancellation tests revealed severe neglect at 15 weeks (see p.219) and improved performance with residual neglect at 41 weeks (see p.167).
Her performance in the inspection time experiment for the left, right and bilateral visual field condition is represented in figures 1a-c below which we will compare to her results in the time bisection task in figure 2.

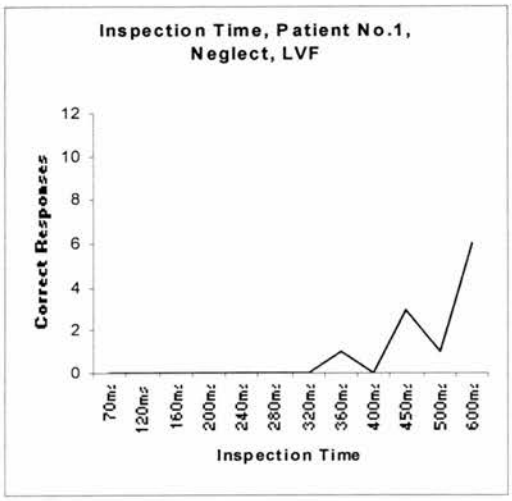

Fig. 1a: Number of correct responses to stimuli presented in the left visual field.

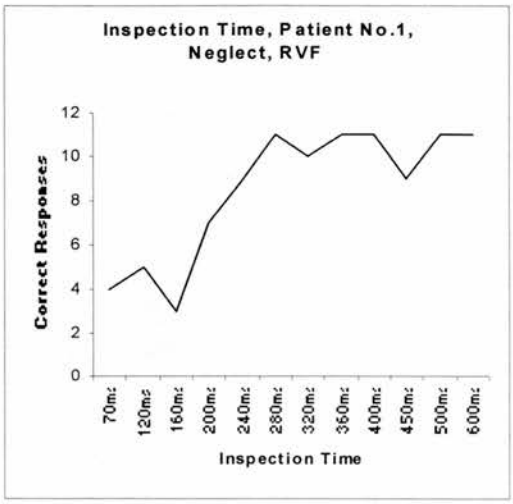

Fig. 1b: Number of correct responses to stimuli presented in the right visual field.

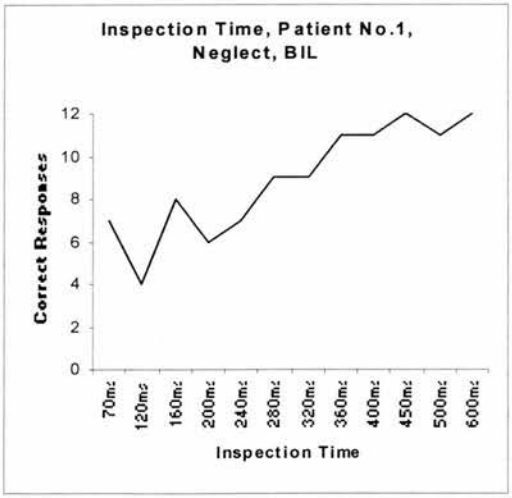

Fig. 1c: Number of correct responses to stimuli presented in the bilateral visual field condition.

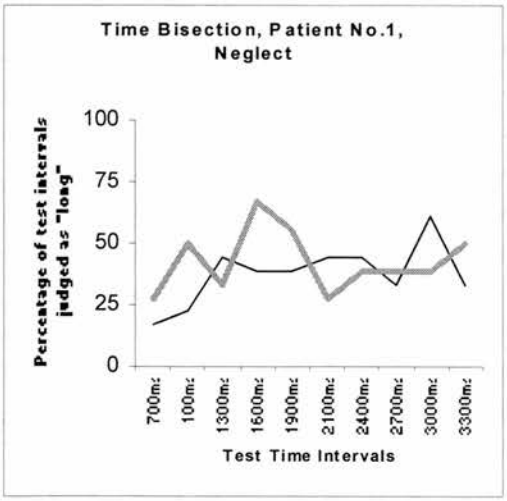

Fig. 2: Time bisection, patient no. 1. The bold line represents the left and the thin line the right ear condition.

The graphs 1a-c demonstrate impaired performance in all visual field conditions which is particularly dramatic when stimuli were presented in the left visual field (see p.226 for comparison with healthy control group). However, consistent responses

were recorded in the inspection time experiment. Interestingly, although the patient's neglect had much improved during the execution of the time bisection experiment, her performance in this paradigm was completely erratic and inconsistent represented by a flat graph in figure 2. It has to be concluded that the task demands were too high for the neglect patient to produce a meaningful response.

- Patient number 2 who also suffered from neglect was tested in three different tests: In the time bisection, rhythm and palindrome reading experiment (at 3, 7 and 8 weeks respectively following cerebral injury). We will only compare the performance in the time bisection and rhythm experiments as the patient did not produce any dyslexic errors. The star cancellation tests demonstrated severe neglect at 3 weeks with steady improvement at 8 weeks (see pp.167, 189, 270).

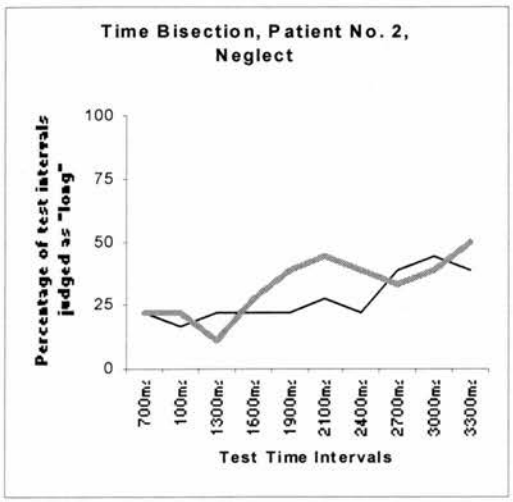

Fig. 3: Performance of patient no. 2 in the time bisection test.

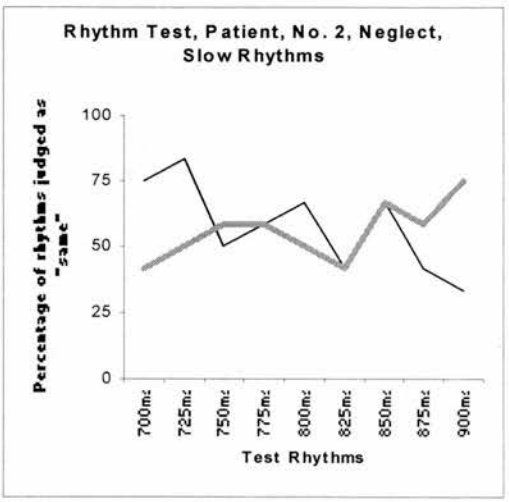

Fig. 4a: Performance of patient no. 2 in the judgement of slow rhythms.

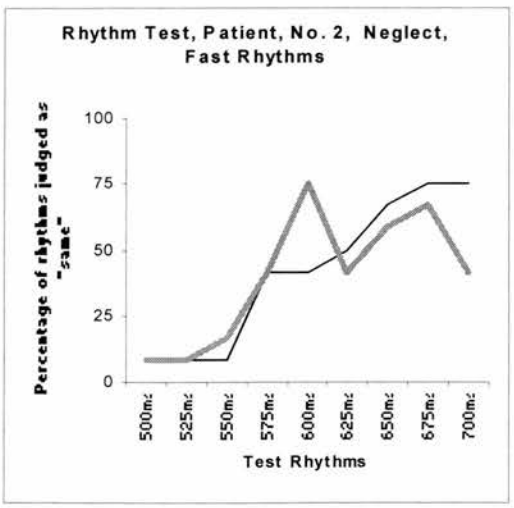

Fig. 4b: Performance of patient no. 2 in the judgement of fast rhythms.

Figure 3 demonstrates again the chaotic response pattern in the time bisection experiment as it was observed in patient no. 1. Instead of an s-shaped curve an almost

flat graph is produced (the bold and thin lines represent left and right ear condition which will not be discussed at this point).
A similarly erratic pattern emerged with the slow rhythms tested four weeks later (fig. 4a) although the patient's neglect had improved which suggests that the discrimination of slow rhythms was too difficult a task for this neglect patient. However, a consistent pattern was observed in the judgement of fast rhythms (fig. 4b; see pp.197, 198 for comparison with the healthy control group) which demonstrates that there was not a global impairment of performance in the neglect patient. Instead the patient displayed sensitivity to different stimuli.

- Patient number 3 suffered from unilateral neglect. She was tested in the rhythm, inspection time and palindrome reading experiment (at two weeks for the rhythm and inspection time and at 8 weeks for the reading experiment). At 8 weeks she still displayed severe neglect (see p.270). Figures 5a and b represent her performance in the rhythm experiment, figures 6a-c her performance in the inspection time experiment.

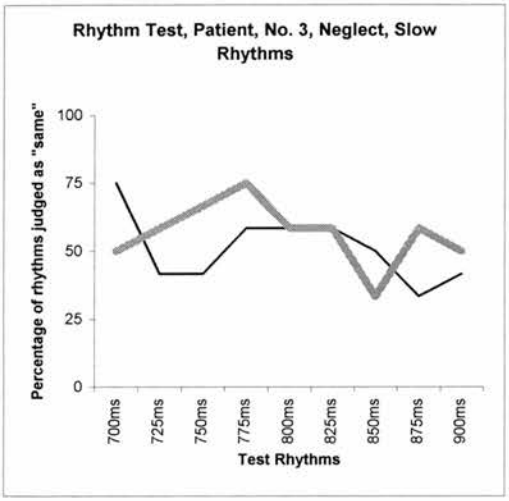

Fig. 5a: Performance of patient no.3 in the judgement of slow rhythms.

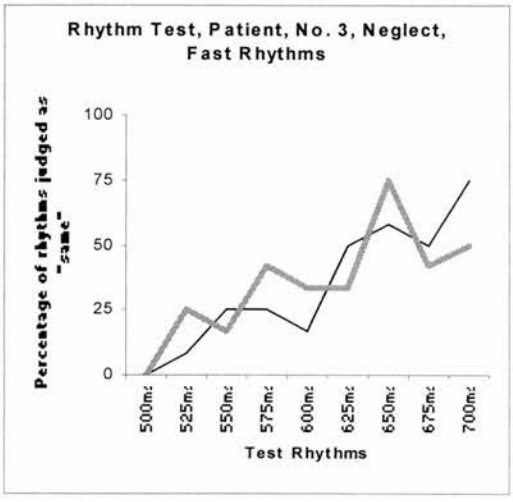

Fig. 5b: Performance of patient no.3 in the judgement of fast rhythms.

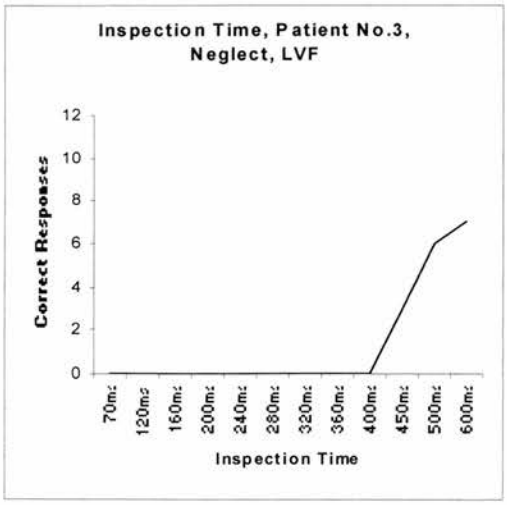

Fig. 6a: Number of correct responses to stimuli presented in the left visual field.

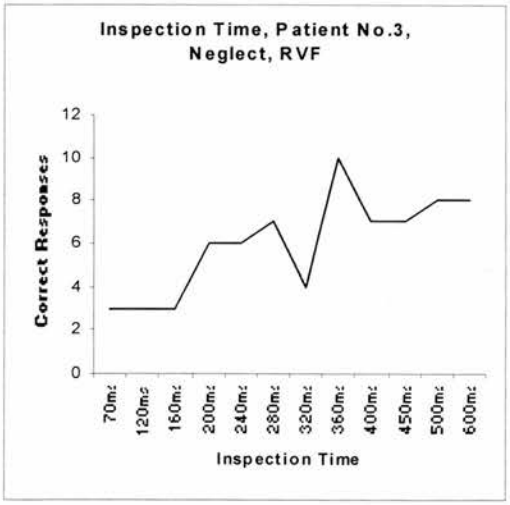

Fig. 6b: Number of correct responses to stimuli presented in the right visual field.

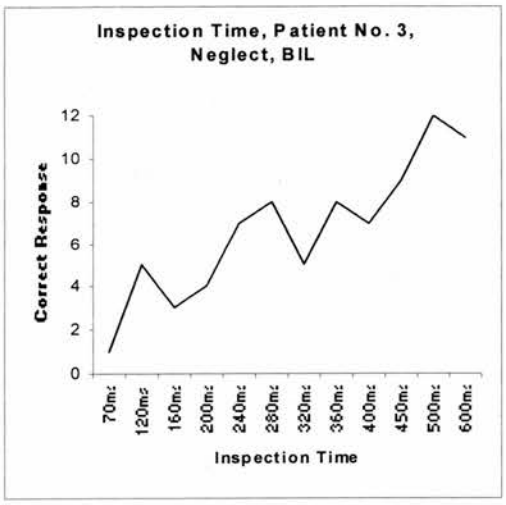

Fig. 6c: Number of correct responses to stimuli presented in the bilateral visual field condition.

As patient number 2, this neglect patient displayed consistent responses for the fast rhythms but is at a loss for rhythms slower than 700 ms.
In the inspection time experiment, an impaired performance is revealed in all visual field conditions. Similar to patient 1, the impairment is particularly drastic in the left visual field.
As for the reading experiment, there was only a minimal impairment. The patient participated in the first reading experiment of palindromic words and non-palindromic words. Out of 72 stimuli altogether, only six were identified incorrectly despite the presence of severe neglect as measured by the star cancellation test.

- Patient number 4 was a neglect patient who was tested in the rhythm (fig. 7a, b) and the two parts of the palindrome reading experiment (at 1 week and at 4 and 5 weeks respectively). Neglect was severe at week 1 with significant improvement between the fourth and fifth week (pp. 189, 270).

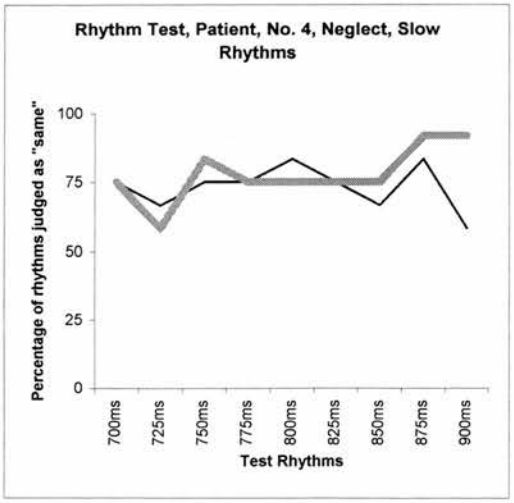

Fig. 7a: Performance of patient no. 4 in the judgement of slow rhythms.

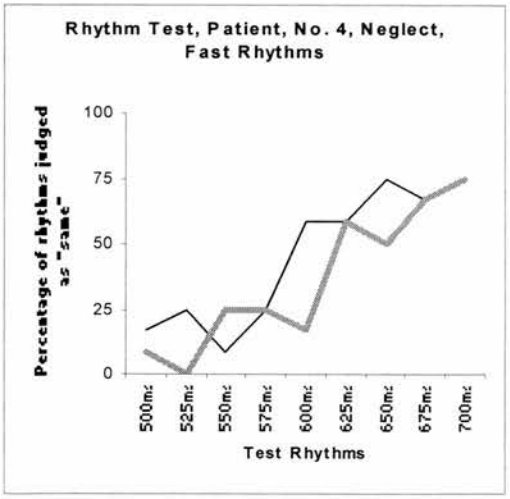

Fig. 7b: Performance of patient no. 4 in the judgement of fast rhythms.

A familiar result was obtained. The perception of slow rhythms was severely impaired (with a tendency to classify the test rhythms as the same as the reference rhythm) whereas the classification of the fast rhythms resembled more the response patterns of the normal control population despite severe neglect.
As for the patient's performance in the reading experiment, she was the subject who produced most errors. In the first part, when asked to read palindromic and non-palindromic words she made 20 errors. There were 76 stimuli in total. A week later, at week five which correlated with improved star cancellation test scores, she only identified incorrectly 7 out of the 72 palindromic and non-palindromic non-words.

- Patient number 8 was a non-neglect stroke patient who agreed to participate in the time bisection and rhythm experiments (at 3 and 5 weeks respectively). Figure 8 represents his responses in the time bisection and figures 9a and b in the rhythm experiment.

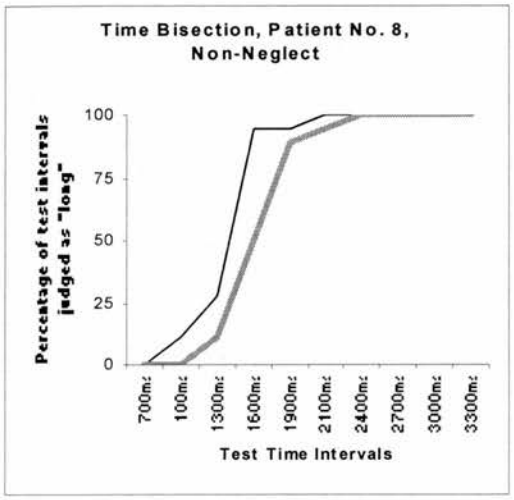

Fig. 8: Patient no. 8. Time bisection experiment.

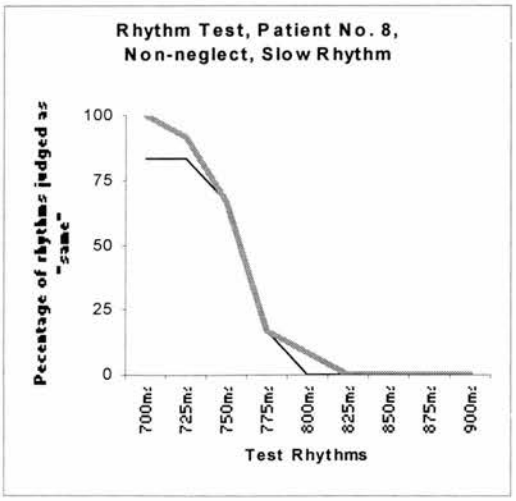

Fig. 9a: Performance of patient no. 8 in the judgement of slow rhythms.

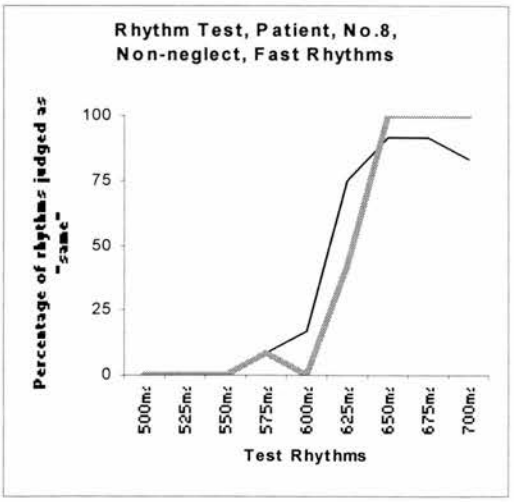

Fig. 9b: Performance of patient no. 8 in the judgement of fast rhythms.

Unlike the neglect patients, patient number 8 is able to give consistent responses not only when judging fast rhythms but also slow rhythms and in the bisection of test time intervals in the bisection task. The graphs resemble very much the ones produced by the non-stroke subjects (see pp. 173, 197, 198 for comparison with the healthy control group).

- Patient number 9 was a non-neglect stroke patient who performed both the rhythm and the inspection time experiment (at 2 and 4 weeks respectively). Figures 10a and b represent her performance in the former and figures 11a-c in the latter experiment.

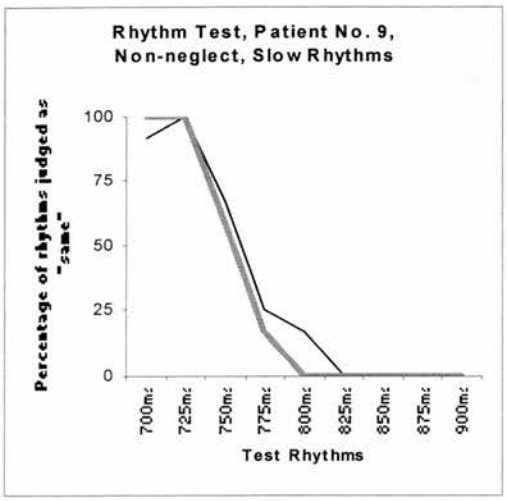

Fig. 10a: Performance of patient no. 9 in the judgement of slow rhythms.

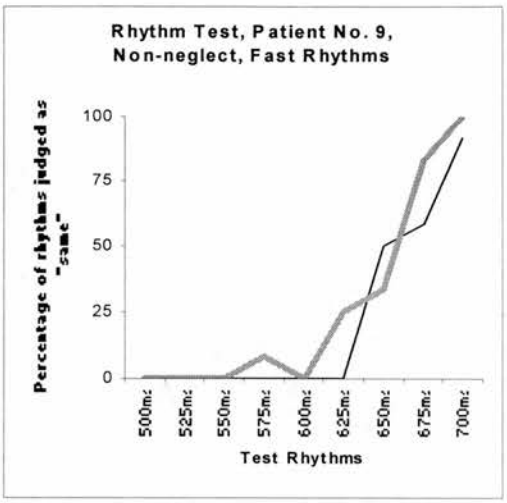

Fig. 10b: Performance of patient no. 9 in the judgement of fast rhythms.

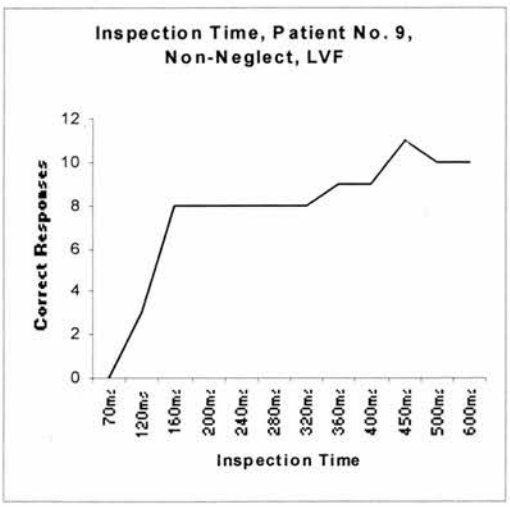

Fig. 11a: Number of correct responses to stimuli presented in the left visual field.

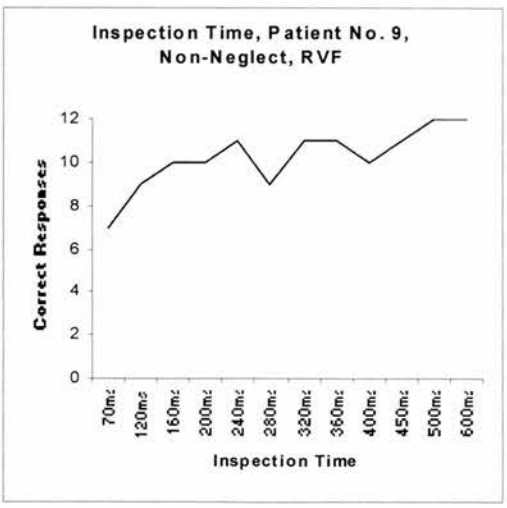

Fig. 11b: Number of correct responses to stimuli presented in the right visual field.

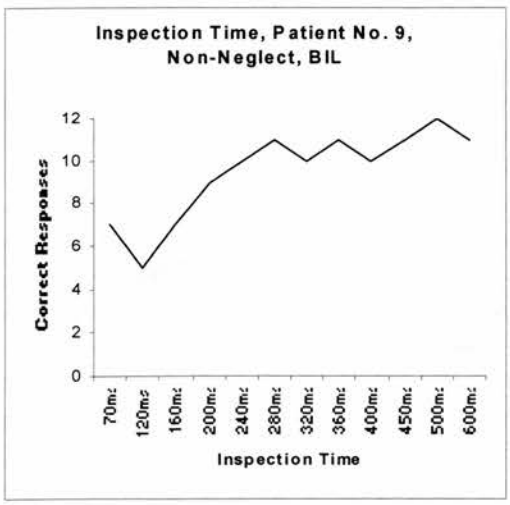

Fig. 11c: Number of correct responses to stimuli presented in the bilateral visual field condition.

As in patient number 8, the graphs representing the performance of patient number 9 in the judgement of the test rhythms resemble the ones obtained from the normal control group - both for the fast and the slow ones.

In the time inspection paradigm, the results of patient number 9 for the left visual field condition demonstrate a dramatically better performance compared to patient number 1 who suffered from neglect (see fig.1a above). The number of correctly identified stimuli remains also higher in the right and bilateral field condition. However, interestingly in comparison with the normal control group, there appears to be an impairment at short inspection times both in the left and bilateral visual field condition (see p. 226).

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